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(Signed).... Graham Dadorn .....

PERMANENT ADDRESS:

Department of Zoology
University of Alberta
EDMONTON, Alberta

DATED... 25 May .....1973.

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THE UNIVERSITY OF ALBERTA

COMMUNITY STRUCTURE AND ENERGETICS IN AN ARGILLOTROPHIC LAKE, WITH SPECIAL REFERENCE TO THE GIANT FAIRY SHRIMP, *BRANCHINECTA GIGAS* LYNCH

© GRAHAM R. DABORN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1973

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Community Structure and Energetics in an Argillotrophic Lake with Special Reference to the Giant Fairy Shrimp *Branchinecta gigas* Lynch submitted by Graham R. Daborn in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Supervisor

.....

.....

.....

.....
External Examiner

Date..23 May 1973.....

ABSTRACT

The life cycles and general biology of three important species in the community of an argillotrophic lake (Fleeinghorse Lake, Alberta) were studied from 1969 through 1972. Particular emphasis was placed on the energetics of the predacious giant fairy shrimp, *Branchinecta gigas* Lynch (Crustacea : Anostraca) and its relations with two main prey species, the anostracan *Branchinecta mackini* Dexter and the copepod *Diaptomus nevadensis* Light.

Eggs of all three species hatched when lake sediments thawed during April, at which time salinity was low as a result of snow melt. Hatching was terminated after a few days as salt deposits redissolved and salinity increased. Periodic samples of lake populations indicated that subsequent patterns of growth were sigmoid in form, with maximum growth rates ranging from 2.1 to 3.2 mm/day in *Branchinecta gigas*, 0.9 to 1.1 mm/day in *B. mackini* and 0.07 to 0.15 mm/day in *Diaptomus nevadensis*. Reproductive capacity was examined by counting the number of eggs present in the ovaries of preserved female *B. gigas* and *B. mackini*. Clutch size was proportional to total length of the female for most of the breeding period (mid-May to mid-June), but decreased again toward the end of the life cycle. Average fecundity of *B. gigas* was estimated to be 936 eggs in 1971 and 460 eggs in 1972.

Numerical abundance of *Branchinecta gigas* in 1972 declined steadily from 3.4/m^2 on 16 May to zero by 19 June, whereas that of *B. mackini* decreased from 154/m^2 on 10 May to 14/m^2 on 19 June. Most of the mortality of *B. mackini* could be attributed to predation by *B. gigas*. Biomass of *B. mackini* rose rapidly during May to a maximum of 542 mg

dry wt/m^2 on 23 May.

Measurements of feeding rate and oxygen consumption by *B. gigas* were made over 24-hour periods in the lake, and of biomass and caloric value from samples returned to the laboratory. Tentative energy budgets were then constructed separately for *Branchinecta gigas* males and females on the basis of logistic growth curves fitted to 1972 field data. In both males and females, 21% of assimilated energy was used in growth, while about 10 and 13% were lost in moulting and non-faecal excretion, respectively. Metabolism represented 55% of assimilated energy in males, and thus corresponded to the sum of metabolism (46%) and egg production (8%) in females.

Various aspects of the internal organisation of the community, its relevance to concepts of ecological theory and its suitability as a subject for system analysis are discussed.

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Dr. Hartland-Rowe identified certain Anostraca; Dr. D. Rosenberg arranged for the identification of the Coleoptera; Hans Boerger identified the Chironomidae and Dr. W. Brooks provided preliminary identification of *Nosema*. Dr. B. Chernik provided much-needed advice on mathematical procedures. To these people I express my sincere thanks.

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INTRODUCTION

During the last three decades there has been a great increase in interest in the energy relations within natural communities. It is assumed that patterns of energy flow through ecosystems are related to the organisation of communities within the systems, and hence that study of energy relationships will provide insight into the mechanisms involved in such community attributes as stability and succession. Furthermore, use of energy concepts in analysing ecological systems provides one common baseline for comparison with other biological, physical and chemical phenomena. Such a holistic viewpoint represents an intellectually more satisfying approach than straightforward documentation of such phenomena. Since almost all of the energy that drives the reactions of the biosphere ultimately comes in the form of sunlight, it is a matter of great importance to examine the ways in which this energy is partitioned among the various components of ecosystems. There is a particular urgency in view of the quantities of energy required to sustain nearly three and a half billion people and the consequent need to interfere with otherwise natural processes of energy transformation and utilisation.

One of the major difficulties faced in the study of ecosystem energetics, however, is the sheer complexity of natural communities. In order to make such studies possible, it is usually necessary either to adopt a number of simplifying assumptions, or to select communities or species that present relatively simple dynamic patterns. In the first alternative, as exemplified by the studies of Verduin (1956), Golley (1960), Engelmann (1961), Odum *et al.* (1962) and Teal (1962),

the fundamental assumption made has been that Lindeman's (1942) conception of trophic levels is valid. As Ivlev (1966) and Engelmann (1966) have pointed out, however, there is scarcely a community in which animals are organised into discrete trophic levels. Many species are omnivorous, while others change their feeding relationships at different times during the life cycle. Thus, this approach is self-limiting and relies heavily on information from the detailed study of single species, either under natural conditions (e.g. Smalley, 1960; Comita, 1964; Golley and Gentry, 1964; Wiegert, 1964; Cummins *et al.*, 1969) or in the laboratory (e.g. Trama, 1957; Richman, 1958; Slobodkin, 1959).

In recent years, attention has moved to the study of artificial ecosystems constructed in the laboratory—the laboratory 'microcosms' of Beyers (1963) and others. Despite their artifactual property, such systems provide a potentially powerful tool for the examination of inter-species relationships and integration. Unfortunately, the approach has so far been unsuccessful in attaining comparable complexity to systems that occur naturally (e.g. Hairston *et al.*, 1968). The study of a relatively simple natural community thus seems to offer a compromise between the detailed analysis desired in laboratory systems and the examination of a natural community without excessive simplification.

The present project was designed to study the distribution of energy within a single species in a simple but natural community. The community is unique to *argillotrophic* lakes—water bodies characterised by extreme turbidity that allows no significant phytoplankton production. There are several such habitats in southern Alberta, and the resident community consists of less than a dozen species. The most spectacular

is the giant fairy shrimp, *Branchinecta gigas* Lynch, which is unique among Anostraca in being both the largest known species, and the only strictly predacious one. Primary food items of *B. gigas* are another species of fairy shrimp and a large diaptomid copepod. Only one generation of each of these species occurs in a year. This fact, coupled with the short life cycle, rapid growth and apparently simple energy relationships indicated that *Branchinecta gigas* was an ideal subject for the field study of energy distribution within a single species.

At the outset, the intention was to obtain a balanced energy budget for an 'average' individual throughout its life cycle. Each of the components of the budget were to be measured independently and, where feasible, under field conditions. Not all of these aims were achieved, but sufficient information was obtained to construct a tentative account of energy distribution during the life of an average male and female, and to indicate the major patterns of change in the partitioning of energy at different stages of the life cycle. In addition, some indication was obtained of the most important pathways of energy flow within the community, and also of the ways in which the several species were integrated to form the community unit.

The fact that this community appears not to be supported by primary production makes it a subject of peculiar interest. While the primary energy source is still uncertain, sufficient evidence is available to indicate the necessary involvement of bacterial production. In this and in other respects, the argillotrophic lake community is eminently suitable both for testing many assumptions regarding ecological

organisation, and for applying the special techniques of system modeling and analysis.

METHODS

Selected physical and chemical parameters of Fleeinghorse Lake were examined to provide an account of the environmental conditions to which members of the lake community were exposed.

Physical

Water temperatures were recorded continuously for extended periods during the spring and early summer of 1970 and 1972 using a Ryan D-30 thermograph. The instrument had a range of -5 C to +25 C and was installed beneath the bridge just west of Provost cemetery (P.C.—Fig. 1). The thermograph was not available for use during 1971. Additional temperatures were also taken using a mercury field thermometer whenever the lake was visited.

Water levels were monitored by reference to a metre stick attached to the bridge, and in association with samples taken at other points in the lake. Secchi disc readings were made regularly using a disc on the end of a metre stick. Specific conductance was measured with a Beckman RB-3 Solu Bridge during 1970, and with a Hydrolab TC-2 Conductivity Meter in 1972.

Chemical

During 1970, 1-litre water samples were taken at the surface near the bridge, and sent the same day to the Provincial Water Analysis Laboratory, Edmonton, for determination of pH, total dissolved solids (T.D.S.), alkalinity, hardness, sulphates, chlorides, orthophosphates, iron and ammonia- and nitrate-nitrogen. In 1972, water samples were stored in a freezer until analysed (in August) at the Water Analysis

Laboratory of the Department of Zoology, University of Alberta. At this time, analysis of ammonia-nitrogen was omitted and that of silicates added. All tests were conducted according to "Standard Methods" (A.P.H.A., 1960).

Biological

For the examination of life cycles, animals were collected with a dip net (1.1 mm pore size) and a #20 Wisconsin-type plankton net at weekly or half-weekly intervals during the months of April, May and June, 1970-1972. Collections were fixed in 10% formalin. All fairy shrimp in these samples were identified and, where possible, sorted according to sex. Large specimens (5 mm and over) of *Branchinecta gigas* and *B. mackini* were placed ventral side up on a wet slide while the total length, exclusive of the uropods (cf. Bowman, 1971 with respect to terminology), was measured to the nearest 0.1 mm with vernier calipers. Smaller individuals were measured using an ocular micrometer in a Zeiss dissecting microscope at a suitable magnification. From each plankton net collection in 1971 and 1972, 100 *Diaptomus nevadensis* were measured by the ocular micrometer method using the Zeiss or a Vickers compound microscope. The specimens were obtained as a random sub-sample, and the developmental stage and sex (where possible) of each was recorded.

During 1972 estimates of the population density of *Branchinecta mackini* were obtained from a series of vertical hauls made with a square net having an aperture of 2116 cm^2 and a pore size of 1.1 millimetres. Three points in each basin were selected by random numbers; at each point the net was inserted by hand at an angle to minimise disturbance

in the water column, and allowed to lie on the lake bottom for three minutes before being raised rapidly to the surface. All fairy shrimp were removed, counted and stored in 10% formalin, and the procedure was repeated on the opposite side of the boat. Both hauls were stored as a single sample, the total number of shrimp collected being multiplied by 2.364 to provide an estimate of abundance per square metre. In most cases there was little or no difference between the two hauls (Appendix IV). During June, as the numbers of *B. mackini* declined and consequently the time required for sorting the samples decreased, the number of samples taken was increased.

Eggs carried by female fairy shrimp that had been examined and measured were routinely removed from the ovisac and counted. These counts could only provide crude estimates of potential egg production, because some eggs from each clutch are normally released from the ovisac on several successive days. Accordingly, it was decided to rely only upon counts of developing eggs that were still in the ovaries. Usually this required the removal of heart and intestine via a dorsal incision, and then the ovaries could be examined *in situ*; occasionally, damaged muscle or parasite infections obscured the view, and it was necessary to remove the ovaries. Heavily infected animals were not used. A total of 97 specimens of *B. gigas* were used for both ovary counts and gut analysis. In order to examine the combined influences of size and age on egg production, 25 to 35 *B. mackini* were taken at random from samples of four consecutive weeks in 1971 and 1972: the number of eggs in the ovaries was then determined as described above.

For determination of wet weights, previously measured *B. gigas*

and *B. mackini* were damp-dried by rolling on filter paper for one minute and then weighed to the nearest 0.1 mg with a Mettler M6 electric balance. Small fairy shrimp were weighed in a Cahn G-2 Electrobalance to the nearest microgram. Dry weights of both fairy shrimp species and of *Diaptomus nevadensis* were determined using the Cahn Electrobalance after drying in an oven at 50±2 C for 24 hours.

Caloric equivalents were obtained using a Parr 1411 semi-microcalorimeter according to the method outlined in Parr Manual No. 128. The animals had previously been measured, dried and weighed. No filling material was used, but several specimens of similar size and sex were used together when the animals were small (all *B. mackini*, *D. nevadensis* and *B. gigas* of less than 40 mm length) in order to bring the sample size above 30 milligrams. Calibration with standard benzoic acid pellets indicated that with the amount of heat evolved from a 30 mg sample, the variation of instrument and method was less than one per cent. Corrections were made for nitric acid production but not for sulphates. The proportion of ash was obtained from 14 samples of *B. mackini* burned at 520 C in a muffle furnace. After weighing, the ashed samples were further incinerated at 925 C to obtain a measure of the remaining carbonates (chiefly $CaCO_3$) present (Cummins and Wuycheck, 1971). Since these carbonates constituted less than 25% of the dry weight, no correction was made (Paine, 1966). There was insufficient material available to repeat the ash determinations with *B. gigas*, and it is assumed that there was no difference between the two species.

Ecological literature is almost replete with statements of the

inadequacy of present methods of measuring oxygen consumption (Kamler, 1970). It is generally agreed that measurements obtained in flow-through respirometers such as those of Olsen *et al.* (1969) and Oertzen and Motzfeld (1969) are superior to closed-bottle methods (Kamler, 1969) and to manometric techniques (e.g. Yokohama and Ichimura, 1969; Livingston, 1970). However, the desire to conduct these measurements in the lake itself precluded methods that required expensive or fragile equipment or a power supply. Accordingly, a closed-bottle method was chosen in association with a modified micro-Winkler technique. The experimental chambers used were wide-mouth glass bottles with ground-glass stoppers, and had capacities of approximately 60, 125, 250, 350, 500, 1,000 and 2,000 ml; the volume of each bottle was determined to the nearest 0.05 ml from the weight of water it held when full at room temperature. For each experiment, the sizes of experimental bottles were selected according to the sizes of animals to be used, and at least one bottle in each series was kept as a control.

Each week, 20 litres of water were taken from the lake, filtered through a #20 plankton net and then boiled for 2 to 3 hours. Boiling caused suspended solids to coagulate and sterilised the water; check measurements with a conductivity meter indicated little change in total dissolved solids after this treatment. After the sediment had settled, the supernatant was siphoned into a covered bucket and allowed to cool overnight with continuous aeration. Several hours prior to the beginning of the experiment streptomycin sulphate was added to the treated water at 50 mg/l to depress bacterial metabolism (Packard and Taylor, 1968; Anderson and Stephens, 1969). It has been shown that a 37 day

period at 200 mg/l streptomycin had no demonstrable effect on *Artemia*, although marked inhibition of growth occurred at 400 mg/l and at 1,000 mg/l streptomycin was lethal (D'Agostino and Provasoli, 1968). All four deaths that occurred during the oxygen consumption experiments were clearly the result of inadequate oxygen, and not of the presence of streptomycin. The bucket of treated water was immersed in the lake for about an hour to equilibrate to lake temperature while sufficient *B. gigas* were collected with a dip-net. Before use, the experimental animals were washed twice in distilled water and once with the treated lake water. Each experimental bottle was filled to overflowing with treated water and two sub-samples taken with 10-ml syringes for preliminary determination of dissolved oxygen concentration according to Burke's (1962) method. This was impractical when the smallest bottles were used, and therefore four controls were set up instead of one: two of these were analysed at the beginning of the experiment and the remaining two at the end. In almost all cases the two samples taken from a single bottle varied by no more than twice the smallest division (0.01 ml) of the tuberculin syringes used for titration with N/40 sodium thiosulphate—an error of less than 10, and usually less than 5 per cent. Variation in oxygen concentration between separate bottles drawn from the same bucket was up to 5 per cent of the average in bottles with volumes of 125 ml or over, but reached 8 per cent in the 60 ml chambers. Other limitations associated with the method are considered in discussion of the results.

The experimental chambers were sealed without inclusion of air bubbles and immersed in the lake at least 10 cm below the surface for

24 hours. All experiments were started in the early afternoon when water temperatures were highest in order to prevent the formation of air bubbles in the bottles. At the end of the experimental period, two 10-ml sub-samples were taken from each bottle and fixed as rapidly as possible; where a measurable decrease in oxygen concentration was found in the control bottles, a comparable correction was applied to the experimental bottles on the assumption that it represented bacterial metabolism. These corrections never exceeded 5 per cent of the measured oxygen depletion in experimental chambers. Experimental animals were fixed and stored separately for subsequent measurement.

Analysis of gut contents in *B. gigas* indicated that two species, *B. mackini* and *D. nevadensis*, together constituted almost all of the food. Attempts to measure feeding rate of *B. gigas* using *D. nevadensis* as prey were unsuccessful, but estimates of feeding rate were obtained from a series of weekly experiments in 1972 using *B. mackini*. Water was taken directly from the lake, filtered twice through a #20 plankton net, and poured into 4.5 litre (1 gallon) plastic containers. Into each a known number of *B. mackini* and a single *B. gigas* were placed; the containers were sealed, then returned to the lake and left for 24 hours. At the end of this time all remaining *B. mackini* were removed, counted, fixed and stored for subsequent measurement, and the number of *B. mackini* missing was considered to be the prey taken by the giant fairy shrimp. One container was always kept as a control (containing *B. mackini* but no *B. gigas*) but no correction for natural mortality was ever necessary.

LIMNOLOGY OF FLEEINGHORSE LAKE

Physical Features

Fleeinghorse Lake is a large, shallow body of water about 2 km southeast of Provost, Alberta (TP 39 R2) at 52° 19' N and 110° 11' W. Elevation of the lake is 655 m (2150') above mean sea level in an area that represents an ecotone between parkland and prairie zones of the western plains. The region is characterised by mixed grassland developed on dark brown soils (Anon, 1969), with occasional aspen (*Populus tremuloides*) woodlots. Annual precipitation averages 28-34 cm (12-14") and with low soil storage capacity (Laycock, 1968) the area must be considered semiarid. Agricultural uses vary from cultivated grain crops to rough pasture.

The lake has no permanent inflow or outlet, receiving most of its annual input of water from snow melt in the early spring, and losing it by evaporation during the following summer. Several gullies that lead to the lake, particularly along the north and eastern shores, carry water only for a week or ten days during April, but effectively drain an area of 20.7 km^2 of cultivated land.

Morphometry. The lake (Fig. 1) is 5.12 km (3.2 miles) in length, with an area of 264.2 ha (652.8 acres) and of irregular shape. Three basins were distinguished for convenience in this study, the East, Central and West basins, having areas of 117.0, 103.2 and 44.0 ha respectively. Depth is almost uniform throughout the east and central basins, varying by no more than 20 cm from one point to the next; the western basin is also of uniform depth, about 30 cm less than the

Figure 1. Outline map of Fleeinghorse Lake, Alberta.

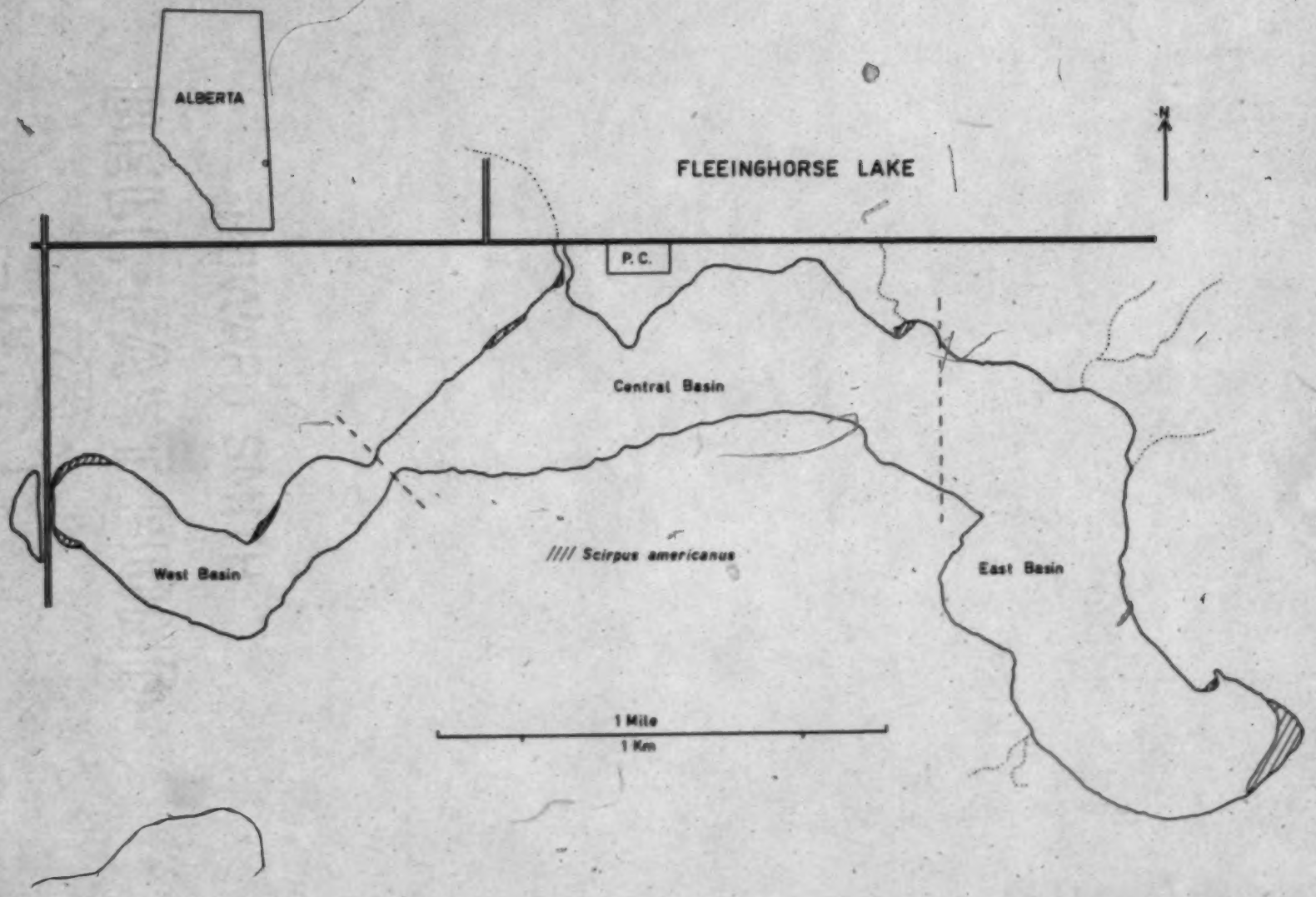
Inset : Province of Alberta with location of lake — O

P. C. : Provost Cemetery.

----- : Dividing boundaries between basins.

····· : Gullies.

Shaded areas : Patches of *Scirpus americanus*.


ALBERTA
FLEEINGHORSE LAKE
N
P.C.
Central Basin
West Basin
//// Scirpus americanus
East Basin
1 Mile
1 Km

other two. Maximum depths encountered just after the spring thaw during the study were 100 to 120 cm in the east and central basins and 70 to 90 cm in the west basin. With greater evaporation than precipitation, these depths declined to about 80 and 50 cm respectively by the middle or end of June.

Bottom sediments over most of the lake consist of mixtures of quartz and clay particles, forming a firm, grey-black deposit with apparently little associated organic matter. Near *Scirpus* beds (see Fig. 1), however, the mud has the texture, appearance and smell of a sapropel. In the latter areas, the organic content of the mud is probably quite high.

Seasonal configuration. As a result of the small volume of water in the basin, the lake has almost no capacity for heat storage. Thus, from the middle of December until the end of March all water and the upper sediments are frozen. Spring thawing began in each of the last three years (1970-1972) during the last week of March or the first week of April, and occurred at the surface of the ice first. Usually, most of the surface ice melted in the west and central basins before any appreciable amount of thawing took place in the eastern basin, because the predominantly westerly winds tended to drive floating ice masses toward the eastern end. This effect delayed the hatching of organisms in the east basin for a week or more after hatching began throughout the remainder of the lake. Despite the presence of large quantities of water in the west and central basins, the bottom sediments remained frozen at least until the middle of April; the presence of large masses of mud-laden ice at the surface was a good indication

that for most species the summer season had begun.

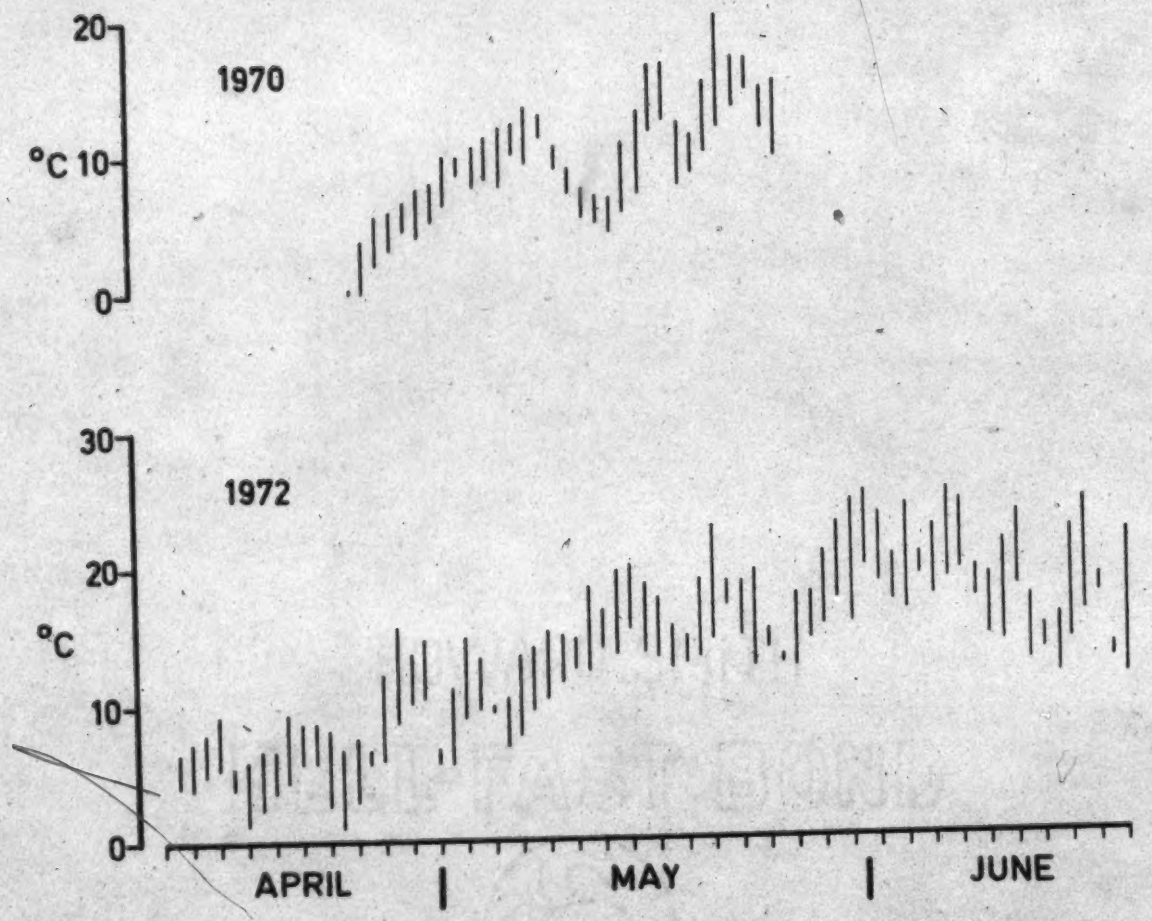
In general, water temperatures closely approximated local air temperatures, the diurnal changes increasing as summer progressed and the volume of water in the basin decreased (Fig. 2). The maximum recorded daily fluctuation was 10 C (19 June 1972) and the highest temperature 28.5 C (28 June 1971).

Following thawing of the bottom sediments, Fleeinghorse Lake water was extremely turbid for the remainder of the open water season. Secchi disc readings varied from 10 to 25 mm, depending primarily on wave action and therefore on wind strength and direction. When water samples were centrifuged for 30 minutes, the compacted sediment constituted between 5 and 7 per cent of the original water volume. Turbidity was greatly reduced if the water was allowed to stand undisturbed for a week, but even after several months some cloudiness remained—probably as a colloidal or bacterial suspension.

Chemical Features

Selection of chemical tests to be conducted was made with a view to characterising the lake as a habitat for aquatic animals. Thus, the methods are essentially 'global' in nature (Dussart, 1967), supported by a few more specific tests. Although differences between the two years for which data are available were probably partly the result of different agencies being involved in the analysis, they are mainly attributable to changes in environmental conditions. At the beginning of April 1970, following lower than normal snowfall and mild temperatures in February and March, the snow remaining on the ground was only

Figure 2. Daily range of water temperatures in Fleeinghorse Lake, 1970 and 1972.


20
°C 10
0
1970
30
20
°C
10
0
1972
APRIL
MAY
JUNE

2-8 cm deep. Snow run-off was therefore light, and water depth in the central basin varied between 80 and 90 centimetres. Following an extremely dry period in April, water depths declined to 60-70 cm by early May. As a result of frequent rainstorms at the end of May and throughout June, water levels fluctuated about these values until July.

In contrast, by the end of March 1972, total winter snowfall was almost 140 cm (about 30% above normal), much of which remained on the ground at the time of the spring thaw. Accordingly, water depths in the central basin in early May ranged between 100 and 120 cm, and with warm weather but moderate precipitation through the next two months, declined slowly to 70-80 cm by the end of June. It is apparent that many chemical variations between and during these years reflect the basic differences in water volume and pattern of precipitation.

Results of the physical and chemical tests conducted in 1970 and 1972 are presented in Figures 3 and 4 respectively. Although no detailed examination for chemical stratification within the water column was undertaken (cf. Eriksen, 1966*a*; Blinn, 1971), the apparent uniformity of temperatures with depth suggested that any such stratification would be of short duration. The general impression is one of total mixing throughout the ice-free season.

Hydrogen ion. With the exception of early spring, when water overlying the frozen sediments had a pH between 7.2 and 7.6, hydrogen ion concentration varied only slightly around a mean of 8.9 in 1970 and 9.3 in 1972. Differences between the two years are probably not significant. In general, the lake is well buffered and drains a relatively small catchment area, so that wide variations in pH would not

Figure 3. Selected physical and chemical features of the water, 1970. Except for pH and specific conductance all units are parts per million.

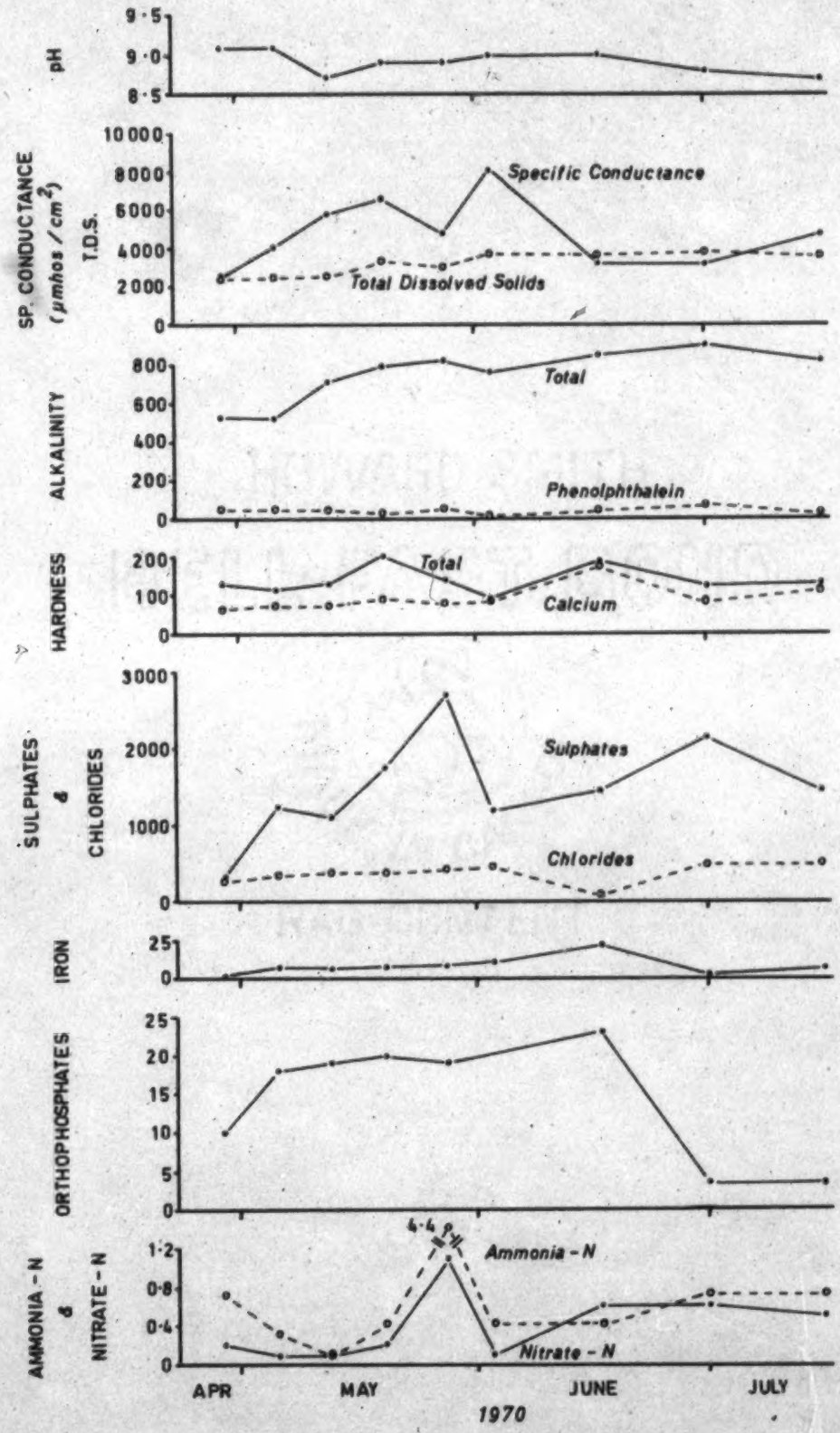
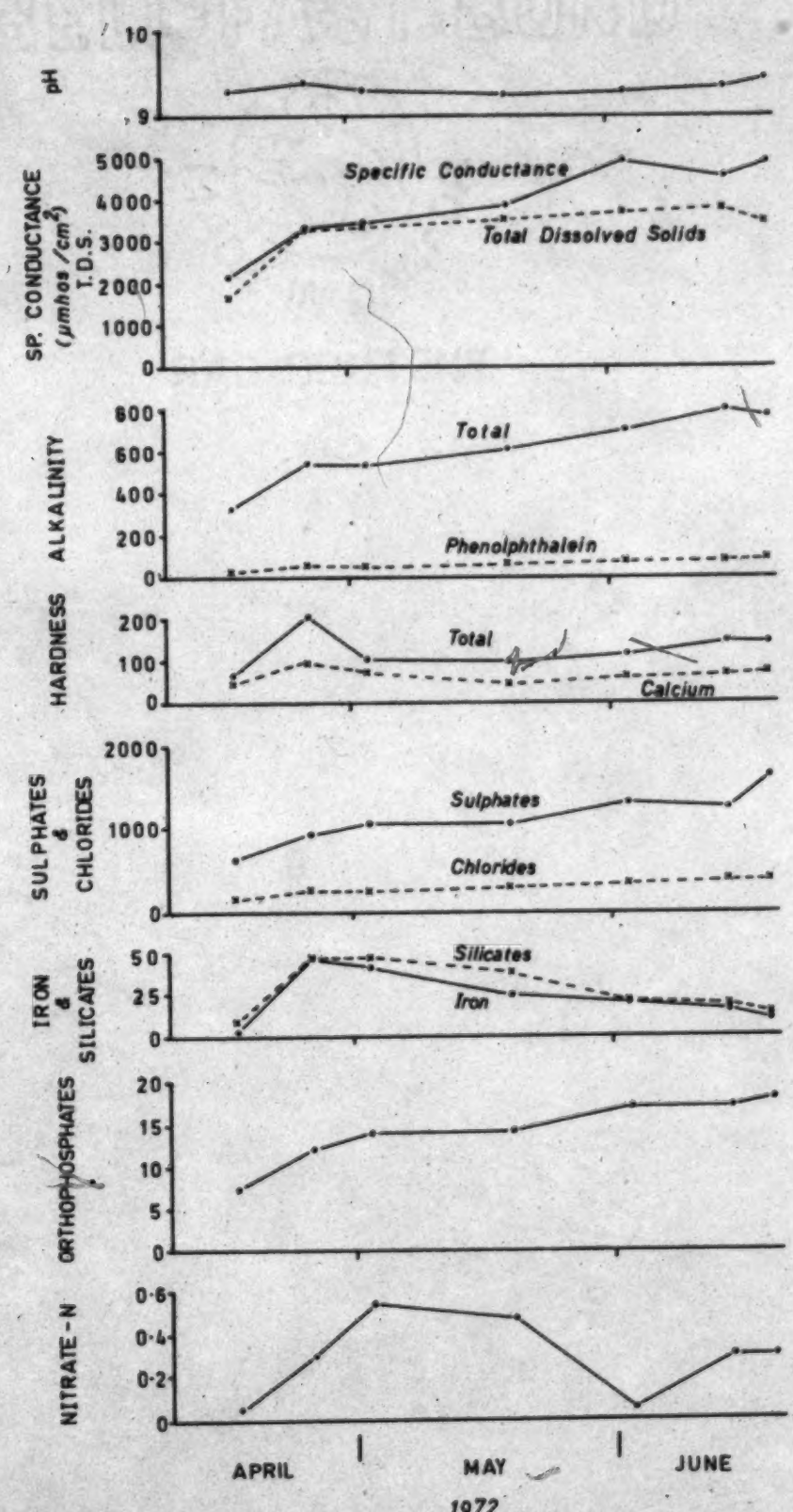

pH
9·5
9·0
8·5
SP. CONDUCTANCE (μmhos / cm²)
T.D.S.
10000
8000
6000
4000
2000
0
Specific Conductance
Total Dissolved Solids
ALKALINITY
800
600
400
200
0
Total
Phenolphthalein
HARDNESS
200
100
0
Total
Calcium
SULPHATES & CHLORIDES
3000
2000
1000
0
Sulphates
Chlorides
IRON
25
0
ORTHOPHOSPHATES
25
20
15
10
5
0
AMMONIA - N & NITRATE - N
1·2
0·8
0·4
0
4·4
Ammonia - N
Nitrate - N
APR
MAY
JUNE
JULY
1970

Figure 4. Selected physical and chemical features of the water, 1972. Except for pH and specific conductance all units are parts per million.


pH
10
9
SP. CONDUCTANCE (μmhos/cm²) T.D.S.
5000
4000
3000
2000
1000
0
Specific Conductance
Total Dissolved Solids
ALKALINITY
800
600
400
200
0
Total
Phenolphthalein
HARDNESS
200
100
0
Total
Calcium
SULPHATES & CHLORIDES
2000
1000
0
Sulphates
Chlorides
IRON & SILICATES
50
25
0
Silicates
Iron
ORTHOPHOSPHATES
20
15
10
5
0
NITRATE-N
0·6
0·4
0·2
0
APRIL
MAY
JUNE
1972

be expected (Daborn and Clifford, in press).

Specific conductance and total dissolved solids. Measurements of the specific conductance and total dissolved solids both represent integrating indices of volumetric changes in the lake. They are little affected by changes in chemical species in the water (within a narrow range of concentration), or by influx of CO_2-laden ground water. Thus, with relatively low water levels in 1970 there were much higher specific conductance values than in 1972. Furthermore, the pattern of steadily increasing concentration during 1972 describes the moderate excess of evaporation over precipitation in the basin, whereas the more widely-varying results of May and June 1970 reflect both the low original volume of the lake and the periodic addition of rainwater (Figs. 3 and 4).

The relationship between specific conductance (K) and total dissolved solids (T), expressed as a ratio (T/K) is rather variable in both years, but particularly so in 1970 (Table I). Since some of the ratio values fall well outside the anticipated range at moderate total salt concentrations, I must doubt the accuracy of some determinations in the first year. In 1972 the ratio fluctuated about a mean value of 0.84, which is close to that obtained from the data of White (1967) for a similar turbid pond in southern Alberta. Nonetheless, the high variation in the ratio supports Williams' (1965) contention that the ratio is unreliable at concentrations below 8,000 $\mu mhos/cm^2$ conductance.

Alkalinity and hardness. In general, total alkalinity increased steadily from the time of spring thaw until mid-summer in both years, reflecting a steady increase in buffering capacity of the water.

TABLE I. Seasonal Changes in the Relationship Between Total Dissolved Solids (T) and Specific Conductance (K) in Fleeinghorse Lake Water, 1970 and 1972

1970		1972	
Date	$\frac{T}{K}$	Date	$\frac{T}{K}$
Apr 28	0.93	Apr 16	0.76
May 5	0.64	25	1.00
12	0.49	May 2	0.98
19	0.50	19	0.91
27	0.63	Jun 2	0.74
Jun 2	0.44	14	0.84
16	1.16	19	0.71
30	1.24		
Jul 15	0.76		

Unlike specific conductance and T.D.S., both of which are largely determined by changes in volume, alkalinity values represent a summary of the acid-base interactions of the lake with its surrounding watershed. The absence of fluctuations in alkalinity during 1970, coincident with wide variation in conductivity, therefore indicates the absence of significant ground-water influx during this period. This in turn results from the saturation deficit of the surrounding soils. In 1970, phenolphthalein alkalinity varied between 20 and 80 ppm, and between April and June 1972 increased steadily from 20 to 110 ppm. Clearly the regular increase was associated with rising total salt concentration and hence of buffering capacity.

Carbonate hardness varied irregularly in 1970 and showed little indication of progressive increase in 1972—as did other parameters examined. From the absolute concentration it is clear, however, that there is much less calcium present than might otherwise be inferred from estimates of total alkalinity (Hutchinson, 1957).

Sulphates and chlorides. Sulphates were by far the most abundant anions in the water, representing up to 50% of the total concentration as indicated by conductivity. High levels of sulphate are naturally present in the soils of this region (Wyatt *et al.*, 1944; Driver, 1965) and this, in the absence of forest cover and humic soils, tends to favour accumulation of sulphates in endorheic lakes (Rawson and Moore, 1944). As water levels fell during the summer months, white crystalline deposits of mirabilite ($Na_2SO_4.10H_2O$) were left surrounding emergent stems of *Scirpus* and other objects close to the water surface. The crystals effloresce when exposed to air and collapse to form a white, anhydrous

powder of sodium sulphate (Govett, 1958). During 1970 sulphate concentrations rose rapidly during May, but then dropped sharply at the end of the month (Fig. 3). The pattern presented during 1970 exhibits a weaker correlation with that of conductivity than might be expected. In 1972, however, sulphate levels continued to rise throughout May and early June in conformity with specific conductance (Fig. 4). This general pattern of increasing concentrations accompanying falling water levels is in contrast to that described by Sublette and Sublette (1967). They found that sulphate concentrations decreased as water levels declined in several playa lakes in Texas. Furthermore, dissolved oxygen concentrations remained fairly high throughout the drying phase and hence the decline in sulphate levels cannot be attributed to bacteriogenic reduction. Possibly it was related to capillary withdrawal of water from the playa basin, which would result in precipitation of sodium sulphate in the surrounding soil (Guthrie and Scott, 1969).

Solubility of sodium sulphate is also controlled by temperature: crystal formation begins at about 2 C and proceeds more rapidly as the temperature approaches zero (Edmondson and Anderson, 1965). Thus, during freeze-up in December, sodium sulphate would have crystallised out, and with reconstitution of water levels and thawing of bottom sediments in spring the powder and crystals would have redissolved.

Compared with sulphates, the total chloride concentrations were relatively low, ranging from 230 to 490 ppm in 1970 and from 160 to 390 ppm in 1972. The difference between the two years reflects the greater volume of water present in 1972. A basic pattern of steadily increasing chloride concentrations accompanying evaporative water loss

is evident during both years.

Other ions. Iron occurred in large quantities in 1970 and even greater amounts in 1972. In view of the high pH, it is almost certain that the iron present could not have been in solution (Ruttner, 1953); probably it was associated with suspended particulate matter either as a precipitated hydroxide (Lee, 1970) or possibly as a gel complex (Shukla *et al.*, 1971). The concentrations measured in both years are comparable with some of the highest values found by Rawson and Moore (1944) in their survey of 53 Saskatchewan lakes.

Silica levels recorded in 1972 were similar to absolute values of total iron, and also exhibited a similar pattern: a sharp rise in April followed by a steady decline in concentration during the next two months. No diatom populations have been detected in the lake at any time during the ice-free period. It seems probable that similar behaviour of iron and silica is not fortuitous, and may represent a complexation between them in association with organic or clay materials (Degens, 1965).

Orthophosphates were consistently very high in both years and showed a general pattern of steady increase during the spring and early summer. The sudden decrease from June to July 1970 is inexplicable. Unfortunately, the behaviour of phosphates under natural conditions is so poorly known that the pattern obtained cannot be more closely analysed. It is most likely, however, that suspended clay and colloidal matter play a major role in the dynamics of phosphate molecules (Williams *et al.*, 1970; 1971).

Ammonia and nitrate-nitrogen were not abundant except on one occasion in May 1970 (Fig. 3). The pattern of both was variable and shows

no particular similarity to other constituents examined. The exceptional values obtained on May 27, 1970 may have been related to fertiliser applications on surrounding fields at that time of year.

Flora and Fauna

The flora of Fleeinghorse Lake is extremely limited. Discrete patches of three-square bulrush, *Scirpus americanus* Pers., occurred at several localities near the edge of the lake (Fig. 1), but in total constituted a small fraction of the total lake area. The species is fairly common in alkaline or brackish habitats in temperate North America (Rydberg, 1932). In addition, prairie bulrushes, *S. paludosus* A. Nels., formed a narrow band 3 to 5 metres in width along many parts of the shoreline, but did not extend to depths exceeding 25 centimetres. Undoubtedly, these two species provide microenvironmental conditions that are of importance to some of the organisms present (particularly *Lestes* spp.), but their net production must be very small in comparison with the total production of the lake.

Only one species of filamentous alga, *Enteromorpha crinita* (Roth, 1882), has ever been collected from the lake, despite extensive sampling. Its distribution is restricted to objects that come within a few centimetres of the water surface—perhaps to a depth at which it will be exposed periodically as a result of wave action. Elsewhere the species is estuarine or intertidal (Collins, 1903; Setchell and Collins, 1908) but exhibits such morphological and physiological variability (Klugh, 1922) that its occurrence in inland alkaline waters is not very surprising. I have collected the species occasionally in other turbid ponds in the Wainwright-Provost area, but not in clear alkaline waters. In

Algeria, Beadle (1943) found *Enteromorpha intestinalis* in several inland lakes of moderate salinity. As a consequence of its extremely limited distribution in Fleeinghorse Lake, *E. crinita* can contribute but little to the overall economy of the community, although it may be of importance to the resident corixid, *Cenocorixa dakotensis*.

During December 1970 and 1971, the water under an ice cover of 15-30 cm contained large numbers of a species of *Phacus* (Euglenaceae). It was evident from the bright green gut contents of the few remaining *Daphnia similis* that at this time *Phacus* formed a major component of its diet. Previous visits in September and October of those years, however, had not indicated the presence of flagellates, and I presume that the population only developed around the time of freeze-up in the autumn. Its significance to the flow of energy within the lake community is problematical. Clearly at this time of year it is of importance to the invertebrates remaining in the lake, but there seems no reason to assume that this is of much consequence to populations developing during the spring and early summer. It is possible that the occurrence of *Phacus* at freeze-up was related to decreasing salinity as the water cooled and sulphates crystallised out. No other phytoplankton species was found in the lake at any time during this study.

More than 30 species of invertebrates have been collected in the course of this project (June 1969 to October 1972), but only eight of these have been found both regularly and in abundance (Table II). A complete list of invertebrate species is given in Appendix I. Because of their qualitative and quantitative importance in the community, and their close interactions, three species of Crustacea were studied in

much greater detail than other organisms present.

The spectacular giant fairy shrimp, *Branchinecta gigas*, was first described by Lynch (1937) from specimens collected in the vicinity of Coulee City, Washington. It also occurs in Nevada and Utah (Dexter, 1953), Montana (Lynch, 1937), Oregon (Fryer, 1966), Saskatchewan and Alberta (Hartland-Rowe, 1965). It has only been collected from extremely turbid water and always in association with *Branchinecta mackini*. *B. gigas* is the largest fairy shrimp known, the greatest recorded length being 126 mm for a female from Nevada (Dexter, 1953), and only one other species, *Branchinecta ferox*, approaches it in size. Unlike the latter, however, which may attain 70 mm in length (Daday de Dées, 1910), *B. gigas* is a unique anostracan in being exclusively predacious throughout most of its life cycle. In association with this mode of life, extensive modifications are evident in the structure of the swimming legs (Fryer, 1966) that are not apparent in *B. ferox* (Brtek, 1959).

Branchinecta mackini is widely distributed in western North America where *B. gigas* occurs, and has recently been recorded in Nebraska (McCarraher, 1970). It has been collected in many localities in southern Alberta and Saskatchewan (Hartland-Rowe, 1965). Following its original description by Dexter (1956), however, no study was made of the species until White (1967) examined a population in a turbid slough near Dowling, Alberta. Recently, Brown and Carpelan (1971) described the environmental conditions controlling hatching of *B. mackini* eggs in a Californian playa lake. Without doubt it is one of the most important members of the community in Fleeinghorse Lake, and is a major food item

TABLE II. Major Members of the Fleeinghorse Lake Community

TAXON	SPECIES	1969	1970	1971	1972
Anostraca	*Branchinecta gigas*	++	++	++	++
	Branchinecta mackini	+++	+++	+++	+++
Cladocera	*Daphnia similis*	+++	+++	+++	+++
Copepoda	*Diaptomus nevadensis*	++++	++++	++++	++++
	Diaptomus sicilis	+++	+++	+++	+++
Insecta	*Notonecta kirbyi*	++	++	++	++
	Cenocorixa dakotensis	++	++	++	++
	Lestes congener	+	+	+	+

Symbols: + = infrequent; ++ = common; +++ = abundant; ++++ = very abundant

of *B. gigas*.

The third species examined in some detail during this study was the large calanoid copepod *Diaptomus nevadensis*. It was first collected from a muddy, "probably alkaline" lake at an elevation of 2,000 m in Nevada (Light, 1938) and subsequently in California, North Dakota and Saskatchewan (Wilson, 1953). According to Wilson (1958), it is the only North American calanoid that seems to be exclusively associated with saline waters. No previous study of its life cycle has apparently been conducted, and since it formed a major component of the diet of *B. gigas*, some important aspects of its life cycle were examined during 1971 and 1972. Recently, however, Anderson (1970*a*) concluded that *D. nevadensis* is probably a predator also, feeding upon the much smaller *D. sicilis* under natural conditions. In Fleeinghorse Lake, *D. sicilis* is somewhat less common than *D. nevadensis*, and in view of its small size, the population probably attains a relatively small biomass.

Daphnia similis is a large, heavy-bodied species with a wide distribution in western North America, particularly in marginal habitats such as temporary, saline or alkaline ponds (Brooks, 1957). It also occurs sporadically in southeastern Europe and central Asia. *D. similis* was the only cladoceran consistently present in Fleeinghorse Lake during this study, but while it was numerous, it formed a minor component of *B. gigas* stomach contents.

Insects are poorly represented in the community, and their trophic relations remain largely a matter of conjecture. *Notonecta kirbyi* (Hemiptera) adults were collected during the latter part of May and were seen *in copula* during June and July; juveniles, on the other hand,

were first found toward the latter part of June. It is not clear where the adults overwintered, or whether the juveniles appearing in June came from eggs laid during the same month. Probably, *Notonecta* preys upon all the large crustaceans in the community, but no direct evidence of this was obtained. *Cenocorixa dakotensis* (Hemiptera) adults and young were usually found during May, June and July, but none were seen *in copula*, and the breeding period remains uncertain. Juveniles were found throughout June and July. The trophic relations of this species are totally unknown, but it may feed to some extent upon moribund fairy shrimp (Anderson, 1970*a*) or on *Enteromorpha crinita*. The two species of *Lestes* (Zygoptera) are certainly predacious, although their size might restrict them to feeding on the smaller crustaceans. They were only collected near patches of emergent *Scirpus*. Chironomid larvae, particularly *Cricotopus* sp., were occasionally encountered in general collecting and appear to be very uncommon in the lake. Three specimens of *Diaptomus nevadensis* were taken that had partially ingested first instar chironomids, but it is unlikely that the chironomids are of any great significance in the general flow of energy through the community.

During May and June 1970, both species of fairy shrimp were found to be heavily infected with an undescribed microsporidan parasite of the genus *Nosema*. Samples taken during May and June 1969 had, however, shown no sign of the infection. Infection rates in 1970 reached 100% in *B. gigas* and 91% in *B. mackini*, and evidence was obtained suggesting that decreases in population abundance during June were partly attributable to increased mortality of infected animals. The infection recurred at a lower level in 1971, and in 1972 infection rates were very low

(less than 10%) in both host species. Details of the epizootic during these years are given in Appendix VII. The species of *Noesma* responsible is currently being examined and categorised (W. Brooks—personal communication).

LIFE CYCLE OF *BRANCHINECTA GIGAS*

At the inception of this study only one previous investigation of the ecology of the giant fairy shrimp had been conducted. White (1967) provided a general outline of the physical, chemical and biological features of Wanek Lake, near Dowling, Alberta, with particular emphasis on the life cycles of *Branchinecta gigas* and *B. mackini*. Unfortunately, subsequent studies were forestalled by the drying out of the lake in 1968 (White and Hartland-Rowe, 1969).

Hatching

Nauplii and metanauplii were collected in Fleeinghorse Lake in 1970, 1971 and 1972 within a few days of thawing of the bottom mud in each basin. The hatching period was apparently restricted to one week or less in any single basin, since nauplii were not found in subsequent collections from the same region; however, since the three basins differed considerably in the time of thawing (see p. 14), hatching of *B. gigas* took place over a protracted period of 2 to 3 weeks in the lake as a whole. Neither White (1967) nor I have been successful in observing hatching of this species in the laboratory, so that the time and environmental relationships of eclosion are unknown. Hatching of the giant fairy shrimp in the field, however, is coincident with that of *B. mackini*, and it may be conjectured that the requirements of the two species are similar: i.e. addition of low salinity water (Brown and Carpelan, 1961—see also p. 56).

Requirements for hatching in other species of fairy shrimp range from a mere, short-lived osmotic shock as attributed to members of the

genus *Branchinecta* (*Ibid.*; Horne, 1967) and *Artemia salina* (Clegg, 1962, 1964), to the complex environmental conditions necessary in *Chirocephalus diaphanus* (Hall, 1953, 1959*a*,*b*,*c*), *Eubranchipus bundyi* (Broch, 1965) and *Streptocephalus seali* (Moore, 1967). Cessation of hatching was probably the result of rising salinity (Brown and Carpelan, 1971) as mirabilite precipitated at the lake edge, and perhaps on the bottom, redissolved. In all 3 years of this study, therefore, hatching took place during the last 2 weeks of April. Nauplii were never found before 14 April or after 30 April.

Growth

Branchinecta gigas hatches as a true nauplius 0.9-1.15 mm in length—about twice the diameter of the egg (0.55 mm). Both the nauplius and first metanauplius exhibit a striking whiteness that subsequently fades as yolk reserves are used up and active feeding begins (at 2-3 mm length). Unfortunately, length measurements form a continuous series, so that it is impossible to distinguish discrete moulting stages after the first metanauplius (Heath, 1924; Weisz, 1947; Baqai, 1963). Accordingly, growth has been treated as if it were continuous. Lengths of specimens and sample means of animals collected periodically from Fleeinghorse Lake during 1970, 1971 and 1972 are given in Figures 5, 6 and 7, respectively. Each point on these graphs represents at least one animal, and occasionally several of equal length.

It is apparent from Figures 5 and 7 that males and females exhibit different growth patterns: the males seem to approach a definite

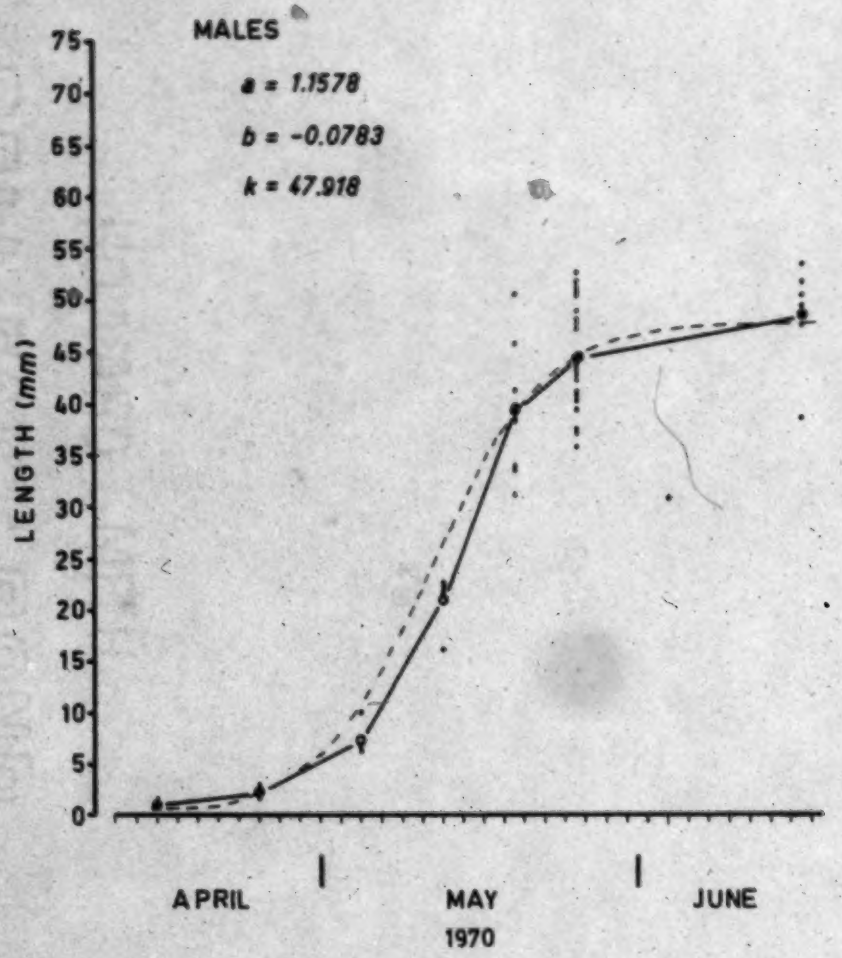
Figure 5. Growth of *Branchinecta gigas* in Fleeinghorse Lake, 1970.

——— Line joining sample means (o)

- - - - Fitted logistic curve (see text)

a, b Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve


MALES
a = 1.1578
b = -0.0783
k = 47.918
LENGTH (mm)
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
APRIL
MAY
1970
JUNE

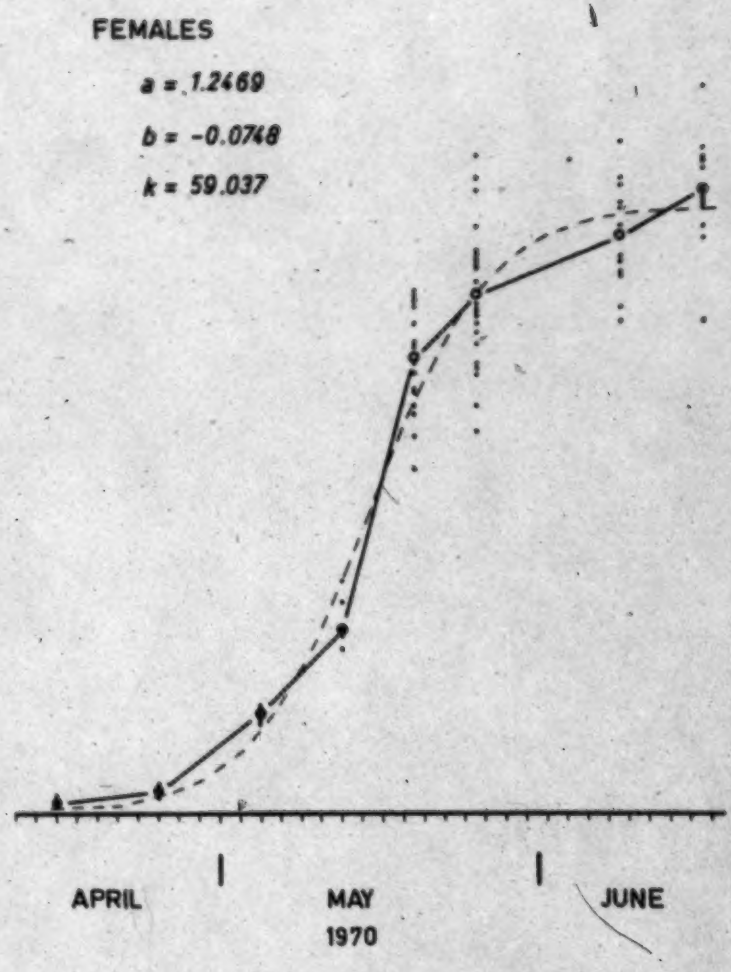

FEMALES
a = 1.2469
b = -0.0748
k = 59.037
APRIL
MAY
1970
JUNE

Figure 6. Growth of *Branchinecta gigas* in Fleeinghorse Lake, 1971.

——— Line joining sample means (o)

- - - - Fitted logistic curve (see text)

a, *b* Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve

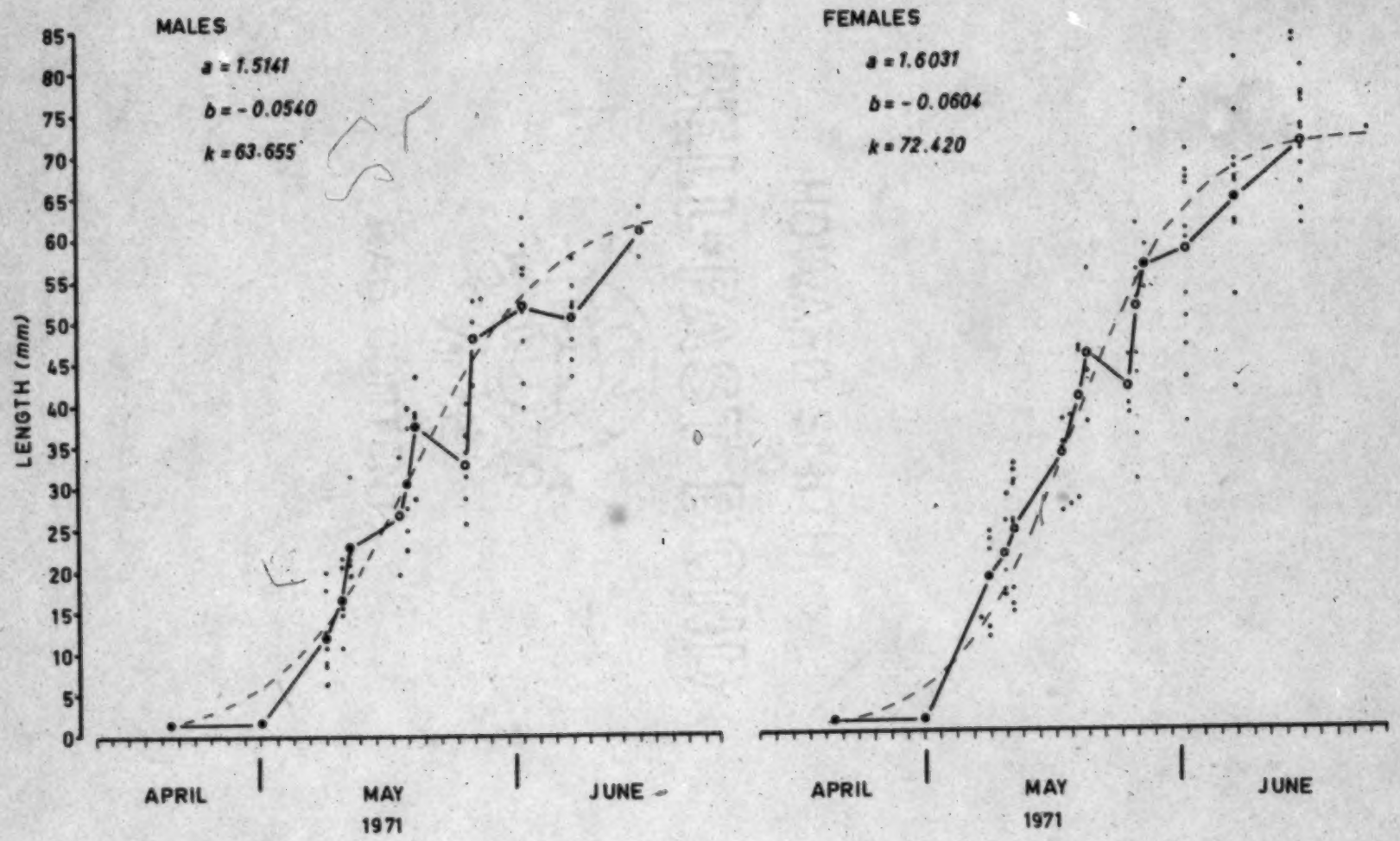

MALES
a = 1.5141
b = - 0.0540
k = 63.655
FEMALES
a = 1.6031
b = - 0.0604
k = 72.420
LENGTH (mm)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
APRIL
MAY
JUNE
1971
APRIL
MAY
JUNE
1971

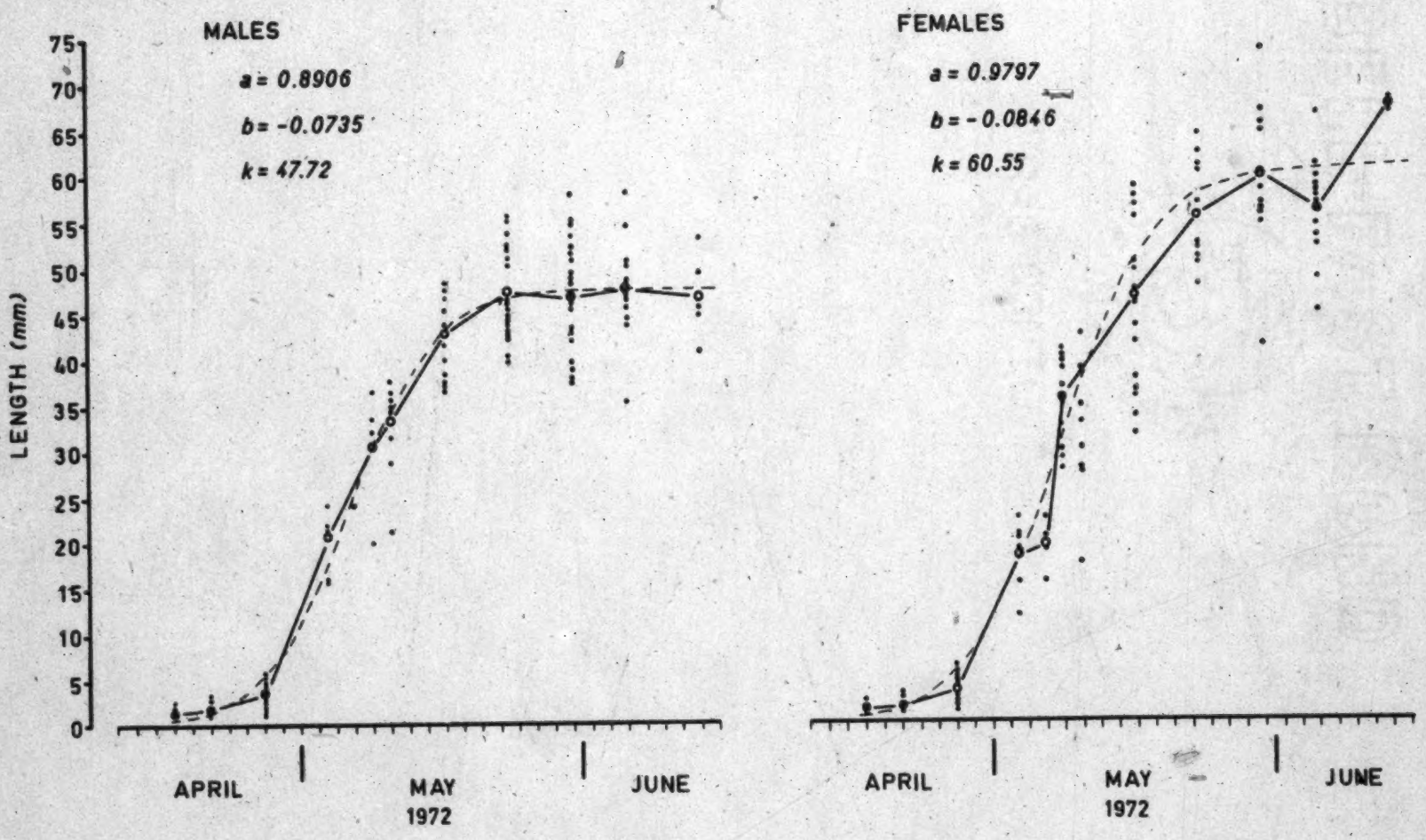
Figure 7. Growth of *Branchinecta gigas* in Fleeinghorse Lake, 1972.

——— Line joining sample means (o)

- - - - Fitted logistic curve (see text)

a, *b* Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve


MALES
a = 0.8906
b = -0.0735
k = 47.72
FEMALES
a = 0.9797
b = -0.0846
k = 60.55
LENGTH (mm)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
APRIL
MAY
1972
JUNE
APRIL
MAY
1972
JUNE

asymptote whereas females continue to increase in length—although at decreasing rates. Presumably such a feature reflects a basic difference played by each sex in the population. Males may grow towards a 'definitive size' which is determined as the size necessary for successful copulation and also for predation upon food organisms that are themselves increasing in size. Females, on the other hand, commit large quantities of energy to the production of eggs—at rates that are correlated with, if not linked to, the size of the animals.

The maximum sizes attained by individuals in the population varied also from year to year. Only two samples were taken in 1969, but both the mean lengths and absolute sizes attained in that year (Table III) were comparable to values recorded in 1971 (Fig. 6). In contrast, average and absolute lengths in 1970 and 1972 were smaller. Although this alternation of maximum size over the four years is rather striking, I assume that it reflects changes in environmental conditions for growth, rather than a feature of the population *per se*.

Increase in average length was slow at first, presumably because of low water temperatures, the extended hatching period, and the extensive morphological differentiation taking place during the first few instars. With reduction of juvenile morphological features, development of secondary sexual characters (5-6 mm length) and adoption of exclusively carnivorous feeding, however, the growth rate increased rapidly. If it is assumed that the growth of an average member of the population is approximately described by the mean lengths of successive samples, the pattern of growth is closely similar to a sigmoid curve. This is less apparent in 1971 when smaller samples were taken at more frequent

TABLE III. Summary of *Branchinecta gigas* Collections from Fleeinghorse Lake, May 1969.

Date	Sex	Number Collected	Mean Length (mm)	Maximum Length (mm)
19	M	5	48.38	52.15
	F	14	62.05	70.75
28	M	2	51.00	60.20
	F	18	77.68	85.85

intervals, and the mean lengths varied considerably as a result of small sample size. There is no evidence of the tri-phasic growth curve deduced by White (1967) for *B. gigas* and *B. mackini*, and by other workers for species of *Eubranchipus* (Dexter and Ferguson, 1943; Coopey, 1950; Dexter and Kuehnle, 1951) and *Streptocephalus seali* (Moore, 1955). In these studies, growth was temporarily retarded at the time that eggs were first extruded into the egg sac, and subsequently resumed after the first clutch was fully developed. Under other conditions, however, anostracan populations both in the field (Moore, 1959, 1963; Dexter, 1967) and in laboratories (Reeve, 1963*a*,*b*; Baid, 1963; von Hentig, 1971) exhibit no such pattern, and it would appear that the tri-phasic growth curve is a facultative rather than an obligate feature.

Several different mathematical formulae have been used to describe the sigmoid growth curve of animals and their populations. Of these, the logistic, Gompertz and von Bertalanffy growth equations have been used most widely, the last forming the basis of yield equations used extensively in fisheries management (Allen, 1969). A comparison of the standard curves with each of the growth curves obtained by joining successive sample means together, using Ricklefs' (1967) method, indicated that the closest fit in all cases was to the logistic curve (Appendix II).

On the basis of Ricklefs' test, therefore, it was assumed that population growth was best described by a logistic curve, and such curves were derived for each of the 1970-1972 generations. The formula used:

$$Y_c = \frac{k}{1 + 10^{a-bx}}$$

where Y_c is the calculated length; x is the age in days; k is the asymptote and a and b are constants defining the point of inflection, and the rate of change in growth rate, is equivalent to that used by Ricklefs (1967). These curves are shown as broken lines in Figures 5, 6 and 7. The values of a, b and k were calculated from the field data and are indicated on each graph. In general, the procedure provides a good fit to the data and shows marked differences only where the sample size was small. The poorest fit was obtained in 1971 (Fig. 6), when mean lengths were based upon frequent, but small, samples; and the best fit was in 1972 (Fig. 7) when sample sizes were relatively much larger.

Given the close approximation of each theoretical curve to the empirical data, it seems reasonable to substitute the values described by the curve for the data itself. In this way one avoids the irregularity determined largely by small sample size and probably attains a closer approximation to the actual growth of an 'average' individual. Curves generated in the same way for *Branchinecta mackini* and *Diaptomus nevadensis* (see pp. 57 and 80) were based upon much larger numbers of animals and, correspondingly, exhibit much closer approximations to the data. On the basis of the fitted curves shown in Figures 5, 6 and 7, the maximum growth rates achieved by *B. gigas* varied from 2.1 to 2.7 mm per day for males and from 2.53 to 3.18 mm per day for females (Table IV).

In all 3 years, the *B. gigas* population disappeared before the end

TABLE IV. Number of *Branchinecta gigas* Collected, and Date, Length and Rate of Maximum Growth as Estimated from Fitted Logistic Curves, 1970-1972

Year	Sex	Number Collected	Date	Maximum Growth* Length (mm)	Rate (mm/day)
1970	Juv.	5			
	Male	50	May 13	28.64	2.10
	Female	75	May 15	30.35	2.53
1971	Juv.	30			
	Male	60	May 15	30.34	2.70
	Female	85	May 17	37.75	3.18
1972	Juv.	54			
	Male	99	May 5	22.52	2.54
	Female	85	May 7	28.60	2.95

*As estimated at the inflection point of fitted logistic curve.

of June, at a time when numbers of *B. mackini* had also declined considerably. Although *B. gigas* obtained a majority of its energy from *B. mackini*, the presence of alternative food organisms, particularly *Diaptomus*, suggests that a simple predator-prey imbalance is not the main reason that the life cycle was terminated at this time (cf. White, 1967). Furthermore, declining egg production in *B. mackini* raises the possibility of senility in that species during June, and observations of *B. gigas* specimens collected during that month indicate a similar decline in 'condition'. It seems best, given present knowledge of fairy shrimp dynamics, to reserve decision on the cause of the disappearance of fairy shrimp towards the end of June.

Length-Weight Relationships

While the length of an animal is a convenient parameter for measurement, the mass of tissue represented by the length is biologically more meaningful. Accordingly, some specimens of *B. gigas* were measured and weighed in order to establish the relationships existing between length (l) and both wet and dry weights (w). Because of technical difficulties associated with determining wet weights of small animals (less than 10 mm), these were omitted. Results are shown in Figures 8 and 9, with regression lines fitted to the data by the least squares method.

The relationship between length (l) and weight (w) may be expressed by the power equation

$$w = ql^b$$

where q is a constant equal to w when l equals unity. On logarithmic coordinates the relationship describes a straight line of the form

Figure 8. Relationships between length (l) and wet weight (w) in *Branchinecta gigas*.

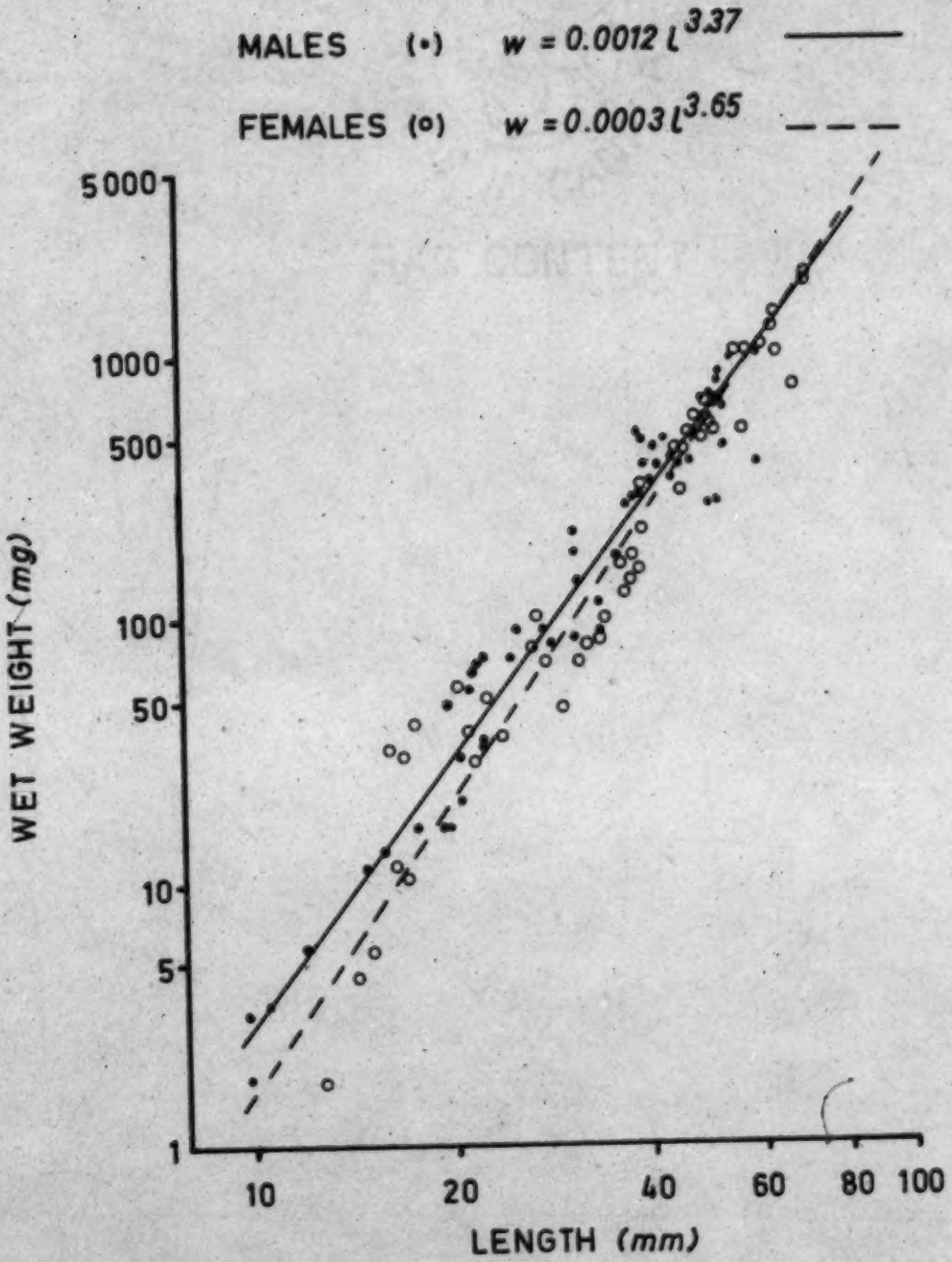
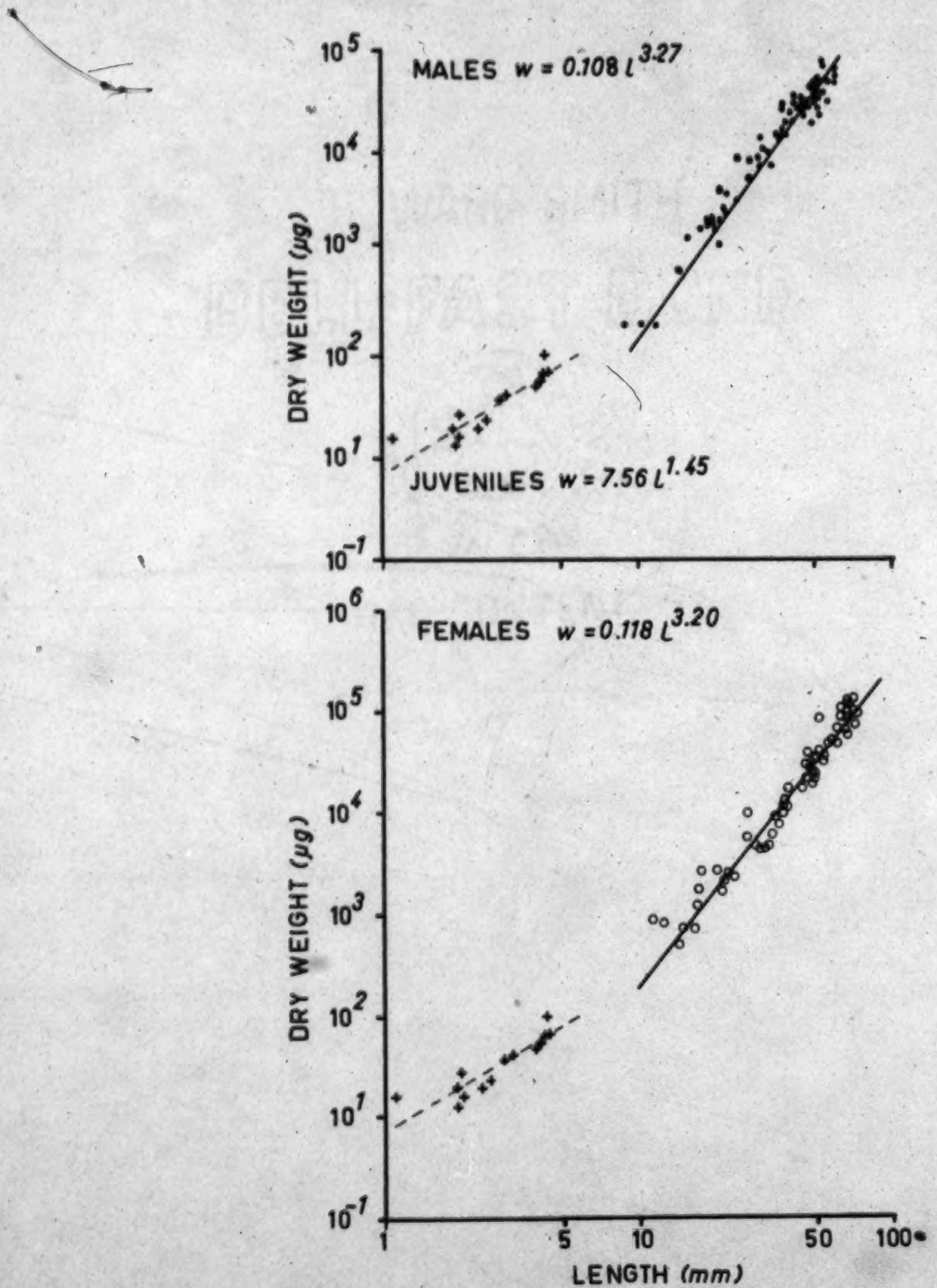

MALES (•) $w = 0.0012\, l^{3.37}$
FEMALES (○) $w = 0.0003\, l^{3.65}$
5000
1000
500
100
50
10
5
1
WET WEIGHT (mg)
10
20
40
60
80
100
LENGTH (mm)

Figure 9. Relationships between length (l) and dry weight (w) in *Branchinecta gigas*.


MALES $w = 0.108\, l^{3.27}$
JUVENILES $w = 7.56\, l^{1.45}$
FEMALES $w = 0.118\, l^{3.20}$
DRY WEIGHT (µg)
10^5
10^4
10^3
10^2
10^1
10^{-1}
10^6
1
5
10
50
100
LENGTH (mm)

$$\log w = \log q + b \log l.$$

When the proportions of the body remain unchanged during growth, the exponent b has the value of 3; a value greater than 3 thus indicates a decreasing ratio of length to weight during the life cycle, and a value less than 3 occurs when growth in mass is relatively less than increase in length (Winberg and Pechen', 1971).

The exponents relating wet weight and length are considerably greater than 3 in both male and female *B. gigas*, indicating that wet weight increased more rapidly than length at greater sizes (Fig. 8). A comparison of the male and female regression lines using the t-test of Simpson *et al.* (1960) indicated that the exponents are statistically significantly different from each other ($p < 0.05$; 105 df). Presumably, part of the greater increase in wet weight of large females was related to egg production. From these data it may be shown that an 80 mm female has a wet weight of 2.48 g and a 60 mm male weighs 1.2 grams.

Changing ratios during the life cycle are also evident in the length-dry weight relationships (Fig. 9), where values of b for males and females are 3.27 and 3.20, respectively. These regression lines are not significantly different from one another ($p > 0.05$; 157 df), which suggests that the significant changes in wet weight of females are primarily associated with increasing quantities of fluids rather than of reproductive or other tissues *per se*. A different length-dry weight relationship occurs with respect to juveniles (Fig. 9). During growth from hatching to the first appearances of sexual characteristics, increase is predominantly in terms of length, the allometric exponent being only 1.45. A change in allometric relation occurs somewhere

between 5 and 10 mm total length.

These data allow conversion of length measurements to either wet or dry weight, whichever is necessary. For example, the greatest rates of growth of 2.70 and 3.18 mm per day for 1971 males and females (Table IV) represent wet weight increments of 37 and 49 mg per day, respectively.

Sex Ratio

The sexes are distinguishable at lengths of 5 to 6 mm when the first external indications of genitalia appear. Subsequent development is characterised by extensive morphological differentiation of secondary sexual characters such as the second antennae. Unlike other species of *Branchinecta*, sexual dimorphism of the swimming legs is not evident in *B. gigas* (Lynch, 1937). As indicated in Table IV, more females than males were caught during 1970 and 1971, whereas the reverse was true in 1972. The numbers are small, however, and there seems little reason to assume a sex ratio other than unity. There is evidence that males tend to die off a little earlier than the females—except, once again, for 1972 (Figs. 5-7). In contrast, in the Wanek Lake study, White (1967) found that males persisted after all females had apparently died.

Reproduction

Egg production begins in *B. gigas* at lengths of 45 to 50 mm and continues through successive broods as the female continues to grow. The reproductive period in Fleeinghorse Lake thus extends through the last 2 weeks in May, and as long as the population persists. Copulation has never been witnessed in this species, but probably occurs shortly

after the contents of the ovaries have been emptied into the sides of the egg sac, as is found in *Eubranchipus* (Pearse, 1913), and therefore shortly after the female has moulted (Packard, 1883). There is no good evidence of synchrony in brood development in the lake population.

White (1967) examined 68 mature females collected from Wanek Lake and demonstrated that the average number of eggs in the egg sac increased with the age (and hence the size) of the animal, to a maximum of 670 eggs in a single brood. Furthermore, his results indicated a decline in clutch size in some of the oldest (estimated at 84 days) animals examined. Difficulties with keeping *B. gigas* under laboratory conditions adequate for observation have meant that information regarding egg production had to be derived from the examination of clutch size in fixed specimens. This, as White (*Ibid.*) noted, is a dubious procedure since some eggs may have been released from an egg sac without noticeably affecting its 'full' appearance. Nevertheless, the maximum actual clutch size is probably represented by the largest clutch sizes counted in this way. The three largest counts made from animals collected from Fleeinghorse Lake during each year of this study are listed in Table V. It is clear from these results that egg production varied considerably from year to year, but was positively correlated with the maximum average length attained by females during a particular season (Table III, Figs. 5-7).

All eggs in a single egg sac exhibit the same degree of shell development. Furthermore, when unshelled eggs had recently been extruded into the egg sac, the ovaries were empty, whereas when the ovisac contained brown, shelled eggs, the ovaries were filled with

TABLE V. Largest Clutch Sizes in Female *Branchinecta gigas* from Fleeinghorse Lake.

Year	Date Collected	Length (mm)	Clutch Size
1969	May 28	82.75	1076
		80.65	964
		85.85	836
1970	June 8	58.75	363
		61.75	328
		52.20	324
1971	June 15	72.20	920
		66.40	836
		67.25	870
1972	May 22	60.15	474
		73.60	411
		64.65	403

large, unfertilized ova. Thus, each clutch represents the total output of both ovaries and it is possible to obtain an estimate of maximum potential clutch size by examination of the number of ova present in the ovaries (cf. Davidson, 1956).

Sexually mature females were therefore dissected and the number of eggs present in the ovaries recorded. The total length of each female was measured, and the data presented in Figure 10 using absolute values for lengths and logarithmic transformations for egg number. Regression lines were fitted by the least squares method. A distinct, positive correlation exists between potential clutch size (as indicated by ovary count) and length of the female, although the scatter of the points indicates that other factors are also involved. In each year, the highest ovary count obtained (978 in 1971; 494 in 1972) corresponded well with the maximum clutch size recorded (Table V). Formulae for the fitted regression lines using transformed data are as follows:

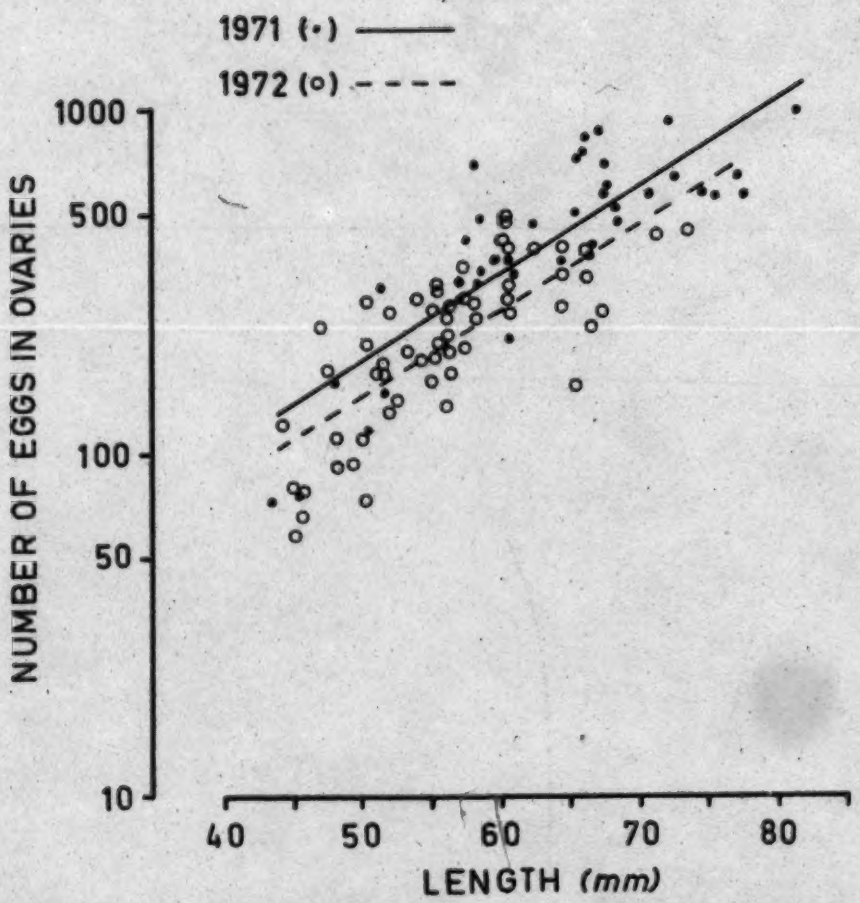
$$1971 \quad \log \text{Egg No.} = 0.9930 + 0.0255\, l$$

$$1972 \quad \log \text{Egg No.} = 0.9311 + 0.0247\, l$$

where l is the length of the animal. The regression coefficients of these lines are not significantly different ($p > 0.5$; 93 df) according to the t-test method of Simpson *et al.* (1960). Presumably, therefore, the rate at which clutch size increased as a function of size remained the same in the two years. The mean difference of the samples, however, is highly statistically significant ($d=6.01$; $p < 0.001$) as one would expect from inspection of Figure 10. On average, clutch sizes were 23% lower in 1972 than in the previous year.

Very little information is available in the literature on the

Figure 10. Relationships between length (l) of *Branchinecta gigas* and number of eggs in the ovaries, 1971 and 1972.


1971 (•)
1972 (○)
1000
500
100
50
10
NUMBER OF EGGS IN OVARIES
40
50
60
70
80
LENGTH (mm)

fertility and fecundity of anostracan populations in the field; indeed, in most studies, even the clutch size of captured females was not recorded. There is some evidence, however, that different genera exhibit different reproductive patterns. According to Linder (1959, 1960) the shell glands of female *Eubranchipus bundyi* undergo a single secretory cycle, with the result that one large clutch is produced when the female first becomes mature, followed by a few much smaller clutches as the glands become 'exhausted'. Field observations tend to support these findings, since maximum clutch sizes recorded for species of *Eubranchipus* are found early in the reproductive period, and are never less than half of the estimated fecundity (Avery, 1940; Coopey, 1950; Moore, 1959). In *Streptocephalus* (Moore, 1955, 1959, 1966; Bernice, 1972*b*) and *Chirocephalus diaphanus* (Lake, 1969) however, clutch size increases as the mature female continues to grow: the largest clutch size recorded in these genera was 902 for *S. dichotomus* (Bernice, 1972*b*). Perhaps a third pattern is represented by *Tanymastix lacunae*, for which Muller (1918—in Lake, 1969) estimated a theoretical fecundity of 17,000 eggs per female.

With one exception, laboratory studies do little to clarify the potential egg production of species of Anostraca—indeed, laboratory estimates of clutch size are frequently exceeded by observations of specimens in the field (cf. Avery, 1940). The exception is a recent study of *Artemia salina* (von Hentig, 1971). By careful experimental work, von Hentig examined the influence of salinity and temperature on egg production and concluded that while the rate of maturation, time of onset of reproduction, length of time between clutches, and total

fecundity were all primarily influenced by temperature, the size of each clutch was mainly determined by the salinity.

The data obtained in the present study provide an inadequate account of potential and actual egg production in *Branchinecta gigas*. To some extent, variations between the two years are a function of differences in maximum attained size (Table IV). Furthermore, no provision could be made for the influence of age (as distinct from size) of animals, although egg counts for all of the largest specimens in each year fall below the regression line fitted for that year. With larger numbers of animals available, however, the influence of age upon fertility was investigated in *B. mackini* (p. 69). Nonetheless, it is clear that egg production of the *B. gigas* population varies markedly from year to year, both as a correlative of maximum sizes attained by females, and as an independent feature. Obviously, egg production is an aspect of an individual's energy budget that may be modified considerably as environmental conditions dictate or permit.

Population Dynamics

Although *B. gigas* has been common in Fleeinghorse Lake in each of the 4 years that I have visited it, restrictions of the methods available for quantitative sampling have made estimates of population abundance difficult to obtain. The method finally chosen sampled a column of water 0.2116 m^2 in area (p. 6), but such a sample was too small to guarantee capture of at least one *B. gigas* at each sample point in 1971. Therefore, an estimate of density had to be derived from the ratio of *B. mackini* to *B. gigas* obtained in a separate series

of dip net samples. As a result of weather limitations, quantitative samples of *B. mackini* could only be taken on two dates in 1971, and accordingly, only two estimates of *B. gigas* abundance could be made. These data are presented in Table VI.

During May and June 1972, however, a complete series of quantitative samples was obtained on each of seven occasions at weekly intervals. Many of these samples contained *B. gigas* and it was therefore possible to estimate the density directly, as indicated in Table VII. Although the numbers are low, a steady decline in abundance is evident throughout these weeks—the low value on May 10 is readily attributable to sample error. Included in Table VII are the estimates of the *B. mackini* to *B. gigas* ratio on each date; these clearly indicate that the structure of the Fleeinghorse Lake community is markedly different from that of Rabbit Dry Lake, California, where the small species outnumber the giant fairy shrimp by up to 40,000 to one (Brown and Carpelan, 1971).

TABLE VI. Estimated Abundance of *Branchinecta gigas*, 1971.

Date	Ratio : $\frac{B.\ mackini}{B.\ gigas}$	No. *B. mackini* per m^2	No. *B. gigas* per m^2
May 19	144	180.7	1.25
June 1	81.3	84.0	1.03

TABLE VII. Estimated Abundance of *Branchinecta gigas*, 1972.

Date	No. Samples Taken	No. *B. gigas* Caught	*B. gigas* per m^2	Ratio : $\frac{B.\ mackini}{B.\ gigas}$
May 10	9	9	2.36	64.9
16	9	13	3.41	34.0
23	9	12	3.15	34.5
30	9	10	2.63	26.7
June 5	14	8	1.35	21.4
14	12	2	0.47	74.5
19	12	0	0	

LIFE CYCLE OF *BRANCHINECTA MACKINI*

While *Branchinecta gigas* is the most spectacular inhabitant of Fleeinghorse Lake, there is no doubt that *B. mackini* is of greater significance to the general economy of the community. Not only does it occur in great numbers and constitute a large portion of the total biomass of the community, but it also represents a major channel through which energy flows and is converted into a form assimilable by the predators: *B. gigas*, *Notonecta kirbyi* and *Lestes congener*.

B. mackini is apparently tolerant of a wide range of salinities, having been recorded from ponds with specific conductance as low as 150 μmhos/cm^2 and as high as 12,000 μmhos/cm^2 (Hartland-Rowe, 1966). Rather than total concentration, however, the factors most responsible for determining its presence or absence in a particular pool may be the relative values of certain anions (Eriksen, 1966*b*). In common with many fairy shrimp species, *B. mackini* exhibits a highly variable morphology from one locality to another, even in the same region. Specimens from Fleeinghorse Lake and many other large, shallow ponds (sloughs) in eastern Alberta, for example, are invariably robust and very opaque, whereas animals from smaller, less turbid pools are often relatively slim in form and translucent. While all specimens conform more or less to Dexter's (1956) original description, there remains some doubt as to the precise taxonomic status of the population in Fleeinghorse Lake (Lynch, personal communication).

Hatching

Hatching began in each year almost as soon as the surface ice began

to melt at the beginning of April, although the largest number of nauplii were collected in each basin when the bottom sediments had thawed. As Brown and Carpelan (1971) noted, the eggs do not normally float, and so presumably pass the winter frozen into the upper sediments of the lake. As the latter thaw, however, many eggs are brought to the surface with fragments of ice and become trapped by surface tension; the result is that *B. mackini* eggs and *Daphnia similis* ephippia can be seen forming extensive windrows several centimetres wide along all downwind shorelines of Fleeinghorse Lake. Probably this represents a considerable mortality factor during the hatching period.

Brown and Carpelan (*Ibid.*) have also shown that two environmental factors interact to control hatching in this species in a playa lake in California. When a temporary depression refills with water, the percentage of eggs that hatch after having remained dry in the mud is determined solely by the salinity of the water. Usually, as salt crystals redissolve the salinity rises rapidly and hatching is terminated until further rainfall lowers the concentration again. In the latter case, the percentage hatching reflects the amount of reduction in salinity. Eggs that have never been dried, however, respond to a combination of salinity and oxygen concentration. A sharp reduction in conductivity stimulates hatching in this case too, but the percentage hatching is greatly increased if the eggs have previously been subjected to a period of low oxygen concentration (less than 2 ppm).

It is difficult to say which of these two cases most applies to the population in Fleeinghorse Lake. Many of the eggs blown up into

windrows show the same indented appearance as dried eggs, although I do not know whether this occurred after they had been deposited on the shore, or as a result of osmotic withdrawal of water as they froze into the sediments in early winter. Certainly, in the latter condition, the eggs would be subjected to a period of low oxygen concentration. Nonetheless, all successful hatching appears to take place within a few days of thawing, and ceases abruptly a few days after the bottom sediments have melted. Samples from late summer and autumn in the last 4 years have shown no signs of late-season hatching.

Because of the delay in thawing of the lake, hatching takes place at intervals of several days in the three basins; thus, for much of the early growth period, individuals are smaller in the east basin than in the west. This effect is partly minimised by the fact that the east basin warms up more quickly once thawing has been completed.

Growth

Nauplii of *B. mackini* (0.45-0.55 mm) were collected over periods of 15-20 days in the latter half of April 1970, 1971 and 1972. As with *B. gigas*, the nauplius and first metanauplius (up to 0.7 mm) were extremely opaque from the presence of extensive yolk deposits, and I presume that feeding began after the second moult, when this opacity disappeared. Growth of an average individual, as defined by the change in mean length of successive samples, was at first slow, but as the water temperature increased and hatching ceased, the average rate of change in length increased rapidly. The growth curves obtained from samples in 1970, 1971 and 1972 are shown in Figures 11, 12 and 13 respectively. Because of the large number of measurements upon which

Figure 11. Growth of *Branchinecta mackini* in Fleeinghorse Lake, 1970.

——— Line joining sample means (•)

- - - - Fitted logistic curve (see text)

vertical rectangle - mean ± 1 s.d.

vertical line - range of sizes

a, b Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve

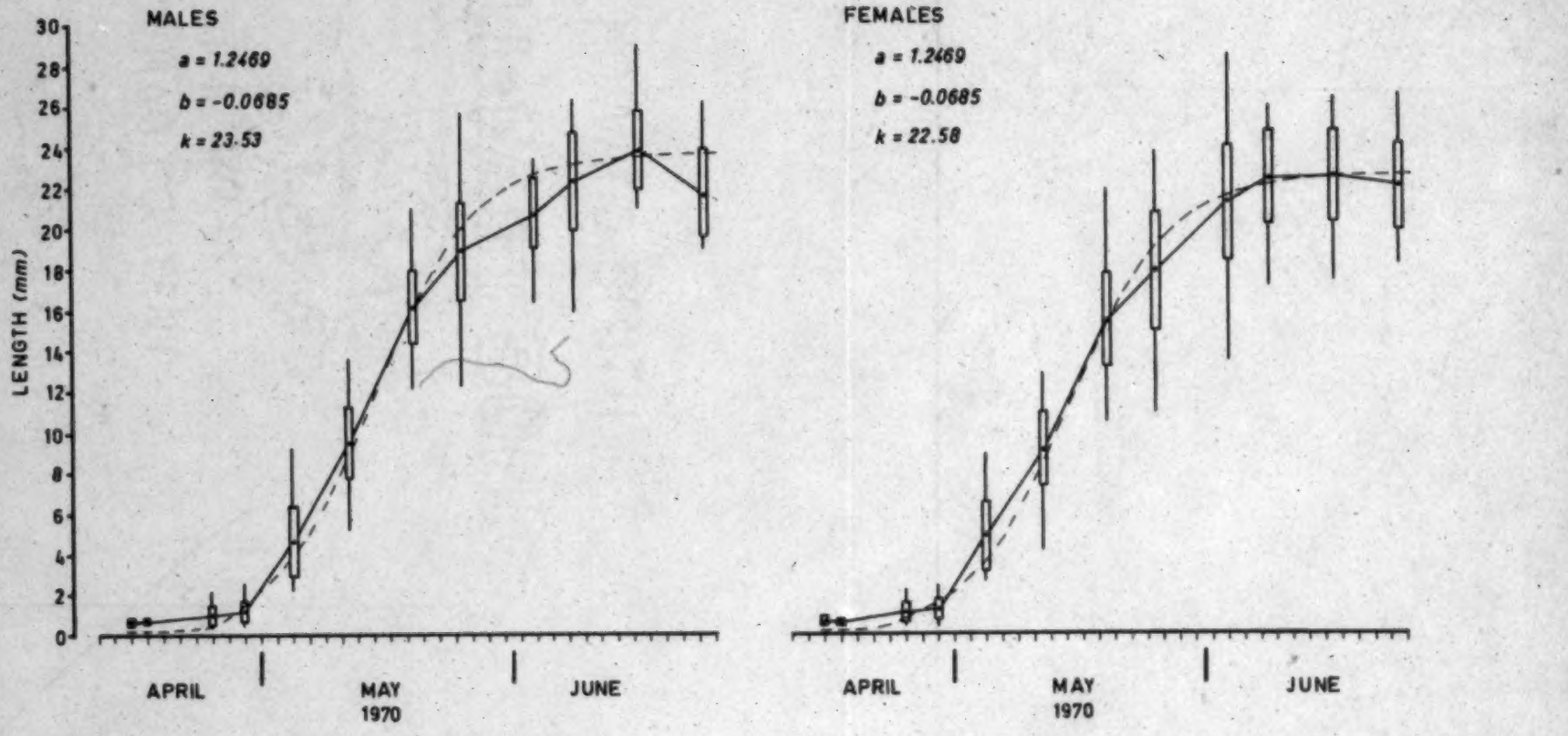

MALES
a = 1.2469
b = -0.0685
k = 23.53
FEMALES
a = 1.2469
b = -0.0685
k = 22.58
LENGTH (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
APRIL
MAY
1970
JUNE
APRIL
MAY
1970
JUNE

Figure 12. Growth of *Branchinecta mackini* in Fleeinghorse Lake, 1971.

——— Line joining sample means (•)

- - - - Fitted logistic curve (see text)

vertical rectangle - mean ± 1 s.d.

vertical line - range of sizes

a, b Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve

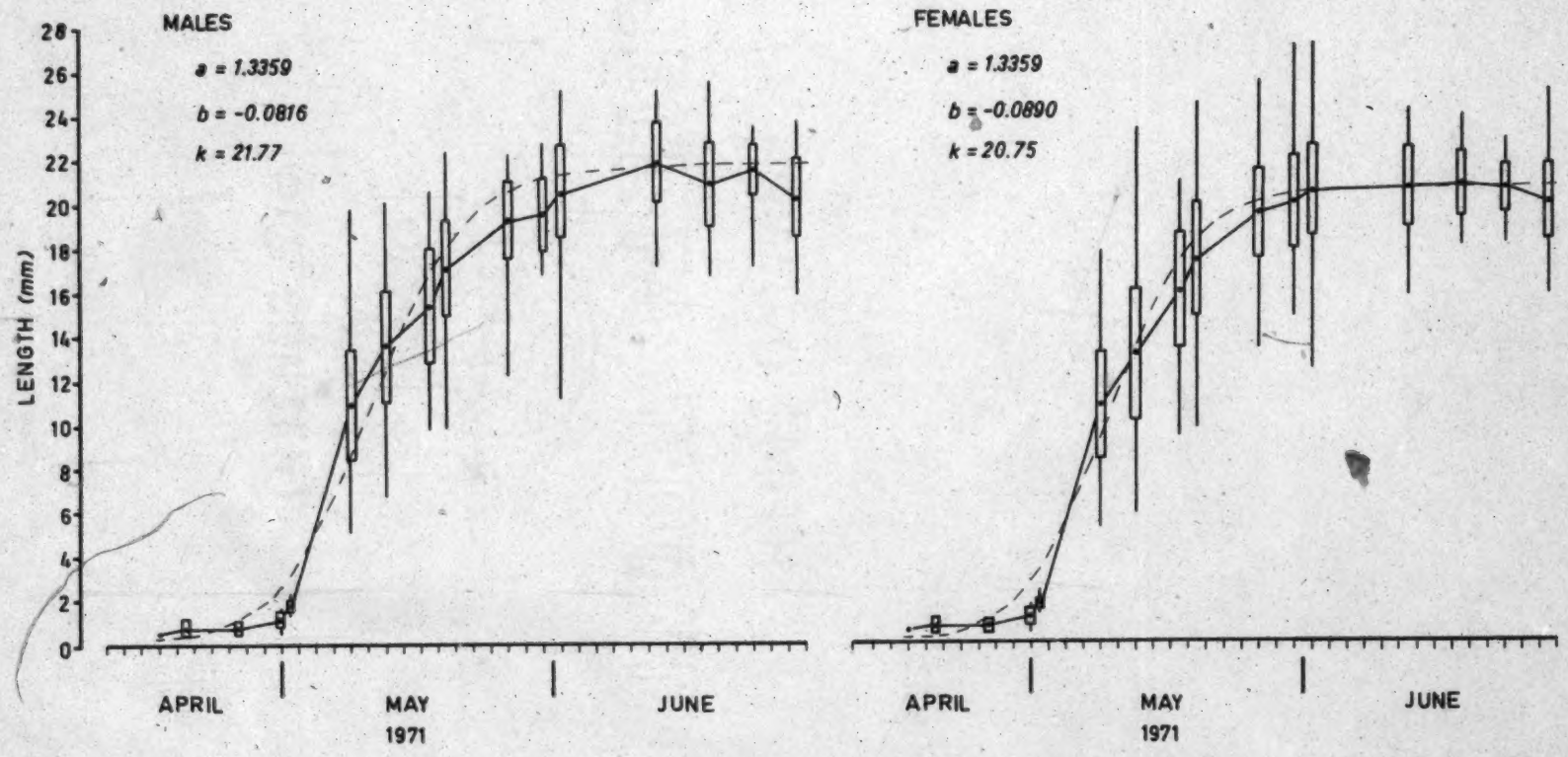

MALES
a = 1.3359
b = -0.0816
k = 21.77
LENGTH (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
APRIL
MAY
1971
JUNE
FEMALES
a = 1.3359
b = -0.0890
k = 20.75
APRIL
MAY
1971
JUNE

Figure 13. Growth of *Branchinecta mackini* in Fleeinghorse Lake, 1972.

——— Line joining sample means (•)

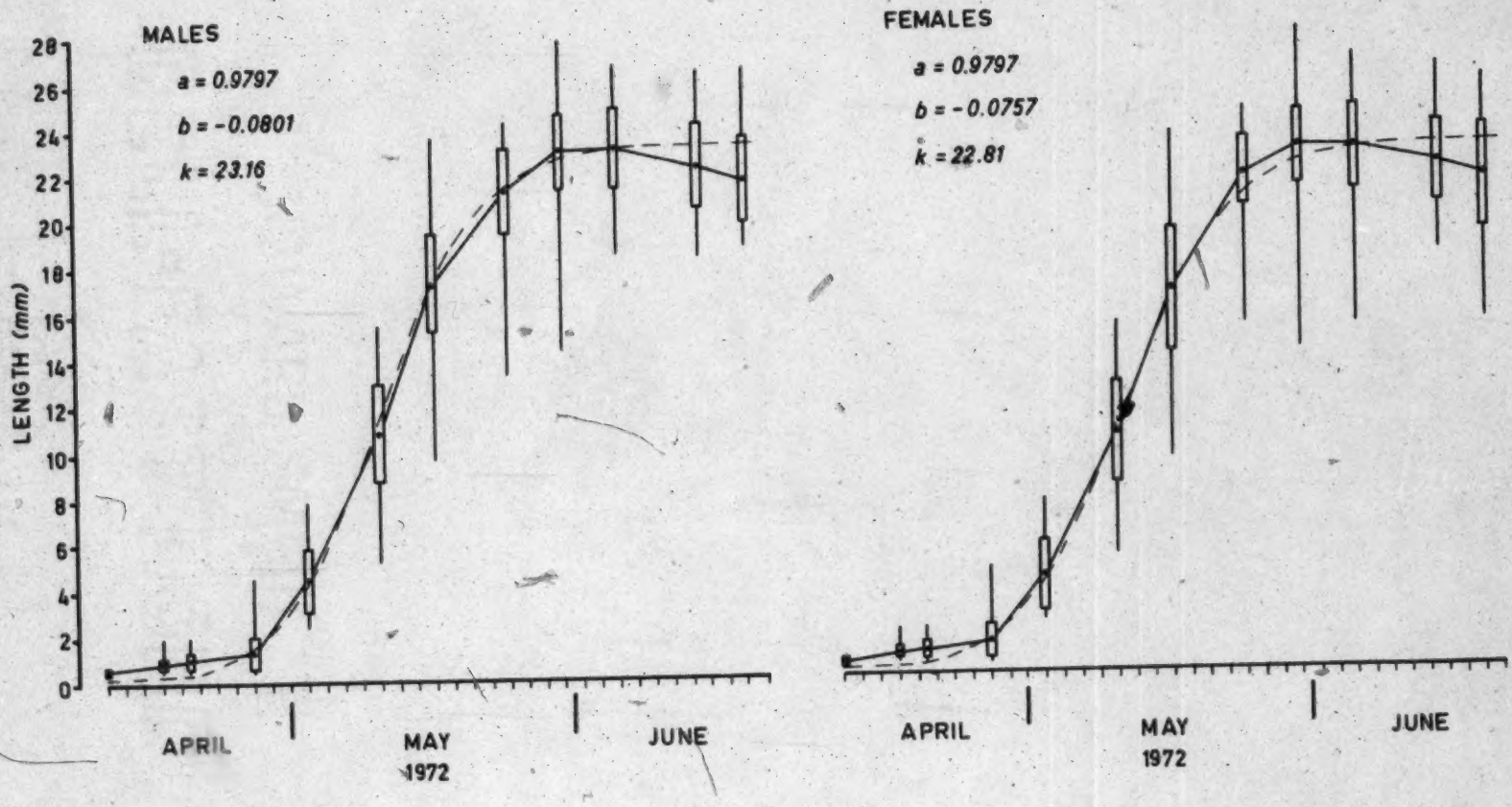
- - - - Fitted logistic curve (see text)

vertical rectangle - mean ± 1 s.d.

vertical line - range of sizes

a, *b* Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve


MALES
a = 0.9797
b = -0.0801
k = 23.16
LENGTH (mm)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
APRIL
MAY
1972
JUNE
FEMALES
a = 0.9797
b = -0.0757
k = 22.81
APRIL
MAY
1972
JUNE

these curves were based (Table VIII), the data have been reduced to show only the mean, standard deviation and range of samples on each date.

The sexes first become recognisable at a length of 2.5 millimetres. As with *B. gigas*, the sample means describe a sigmoid curve in which the asymptote varies according to sex and year. Unlike the larger species, however, *B. mackini* males attain slightly greater lengths than females, and there is no tendency for average female lengths to continue increasing after the males have stopped doing so. On the contrary, sample means for both sexes tend to decline in value after the middle of June as the largest and oldest members die and the remaining population is composed of somewhat smaller individuals.

Use of Ricklefs' method (1967) indicated that a logistic curve provided the closest fit to the observed pattern of growth (Appendix II). Accordingly, such a curve was generated for each sex and each year. The curves are shown by broken lines on the appropriate graphs, and constants used in their calculation are also shown. For comparison, data obtained in 1969 are given in Table IX. It is probable that the low mean lengths of samples in that year are not representative of the maximum lengths achieved; on the contrary, mean lengths of samples on 19 and 28 May 1969 are close to those obtained on similar dates in the next 3 years.

The curves generated in this way seldom fall more than one standard deviation from the sample means and in 1972, when the observed growth curve was based upon measurements of nearly 3,000 animals, the fit of the derived curve to the line joining sample means is so close that

TABLE VIII. Number of *Branchinecta mackini* Measured, and Date, Length and Rate of Maximum Growth as Estimated from Fitted Logistic Curves, 1970-1972.

Year	Sex	Number Measured	MAXIMUM GROWTH* Date	Length (mm)	Rate (mm/day)
1970	Juv.	284			
	Male	421	May 15	12.50	0.92
	Female	506	May 15	12.00	0.89
1971	Juv.	45			
	Male	1084	May 11	11.52	1.02
	Female	1187	May 11	10.36	1.06
1972	Juv.	1132			
	Male	784	May 11	12.39	1.06
	Female	1071	May 11	11.46	0.99

*As estimated at the inflection point of fitted logistic curve.

TABLE IX. Mean Lengths of *Branchinecta mackini* Collected in 1969.

	MALES		FEMALES	
Date	No. measured	Mean Length (mm)	No. measured	Mean Length (mm)
May 19	163	16.23	192	16.20
28	100*	18.21	100*	18.37
June 24	75	18.09	145	17.82
July 2	34	18.91	34	18.63

*Sub-sample only measured.

it is obscured for much of its course. It is appropriate, therefore, to assume that the growth of an 'average' member of the population is represented by the fitted curve. The maximum rates of growth thus obtained are included in Table VIII. Adoption of the formulated curve rather than the empirical one necessarily assumes that the samples were derived from a population that was normally distributed with respect to body length. Inspection of the figures, however, indicates that this was not the case, even though the population was essentially a single cohort. In April the mean length is closer to the lower end of the observed range because of the extended hatching period, whereas by the end of May, the distribution was skewed toward the upper end of the range as older individuals ceased growing while younger ones continued to do so. This feature aside, the deviation of the data from normality is not a very serious objection for substitution of the derived curve for that observed.

The poorest fit is evident in 1971 (Fig. 12). During that year, growth slowed down earlier than expected and the asymptote was rather lower than in 1970 or 1972. I do not feel that this variation in pattern should be attributed to a tendency toward the tri-phasic pattern discussed earlier with reference to *B. gigas*, particularly since it is more apparent in males than in females (see p. 39).

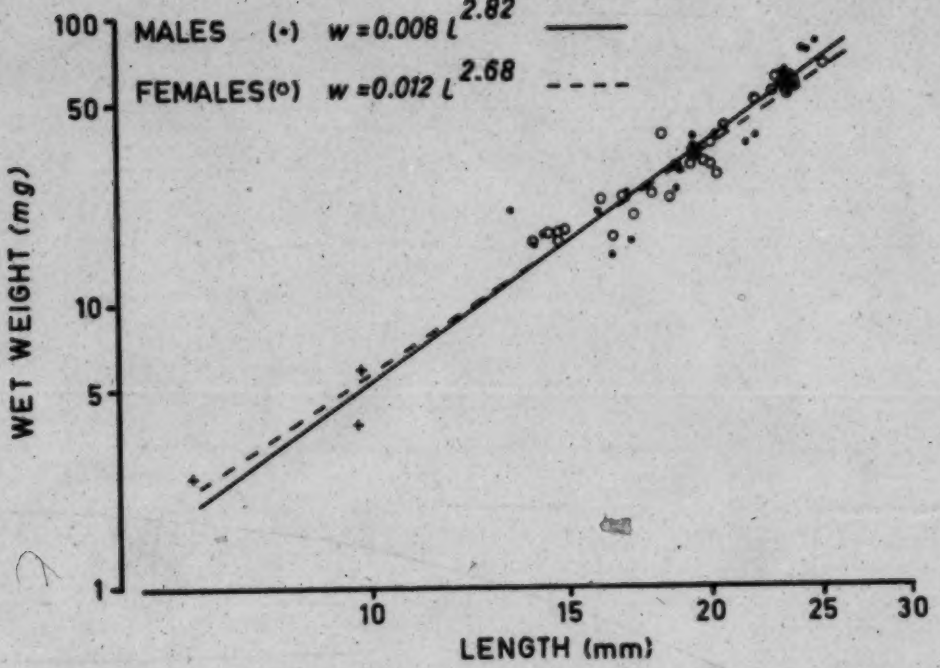
Length-Weight Relationships

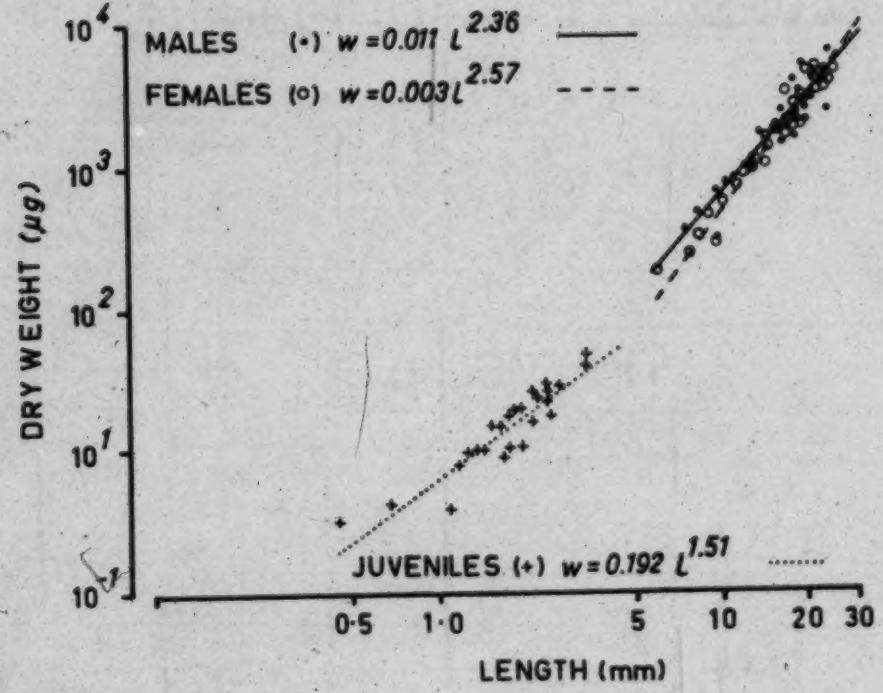
An exponential relationship exists between the body length of *Branchinecta mackini* and either wet or dry weight. When transformed into logarithmic form, the data fall close to a straight line, as shown in the graphs of Figure 14. Because of difficulties associated with

Figure 14. Relationships between length (l) and weight (w) in *Branchinecta mackini*.

Upper graph - Wet weight to Length relationships.

Lower graph - Dry weight to Length relationships.


MALES (•) w = 0.008 l 2.82
FEMALES (○) w = 0.012 l 2.68
WET WEIGHT (mg)
100
50
10
5
1
10
15
20
25
30
LENGTH (mm)


MALES (•) w = 0.011 l 2.36
FEMALES (○) w = 0.003 l 2.57
JUVENILES (+) w = 0.192 l 1.51
DRY WEIGHT (µg)
10 4
10 3
10 2
10 1
10 -1
0·5
1·0
5
10
20
30
LENGTH (mm)

damp-drying small (up to 10 mm) specimens, only three such values were obtained. These indicate no change in the wet weight relationship over the range of lengths from 7 to 30 millimetres. The different exponents *(b)* obtained for wet weight of males and females (2.82 and 2.68, respectively) are not significantly different from each other ($p > 0.1$; 57 df), but do indicate a declining weight to length ratio at greater lengths (Winberg and Pechen', 1971).

In contrast, the exponents obtained for males and females with respect to dry weight (2.36 and 2.57) are significantly different from each other ($p < 0.02$; 63 df), and are somewhat lower than those relating wet weight and length. It would appear, therefore, that much of the increase in weight of the larger males is associated with fluid rather than deposition of discrete tissue. Interestingly, the opposite case applied in *B. gigas* (p. 45).

Juveniles up to 4 mm in length exhibit a totally different length-weight relationship, as might be expected, since early growth involves extensive morphological differentiation and increase in length, rather than deposition of muscle or other internal tissues. While sex may be determined at 2.5 to 3 mm, major development of reproductive systems probably begins with the change in allometry evident at lengths of 4-7 millimetres. In this respect, the patterns of growth of *B. mackini* and *B. gigas* are similar: the exponential relationships between length and dry weight are almost equal in juveniles (1.51 and 1.45, respectively), and the change in allometry in each species occurs at lengths a little greater than those at which sex may first be determined.

Sex Ratio

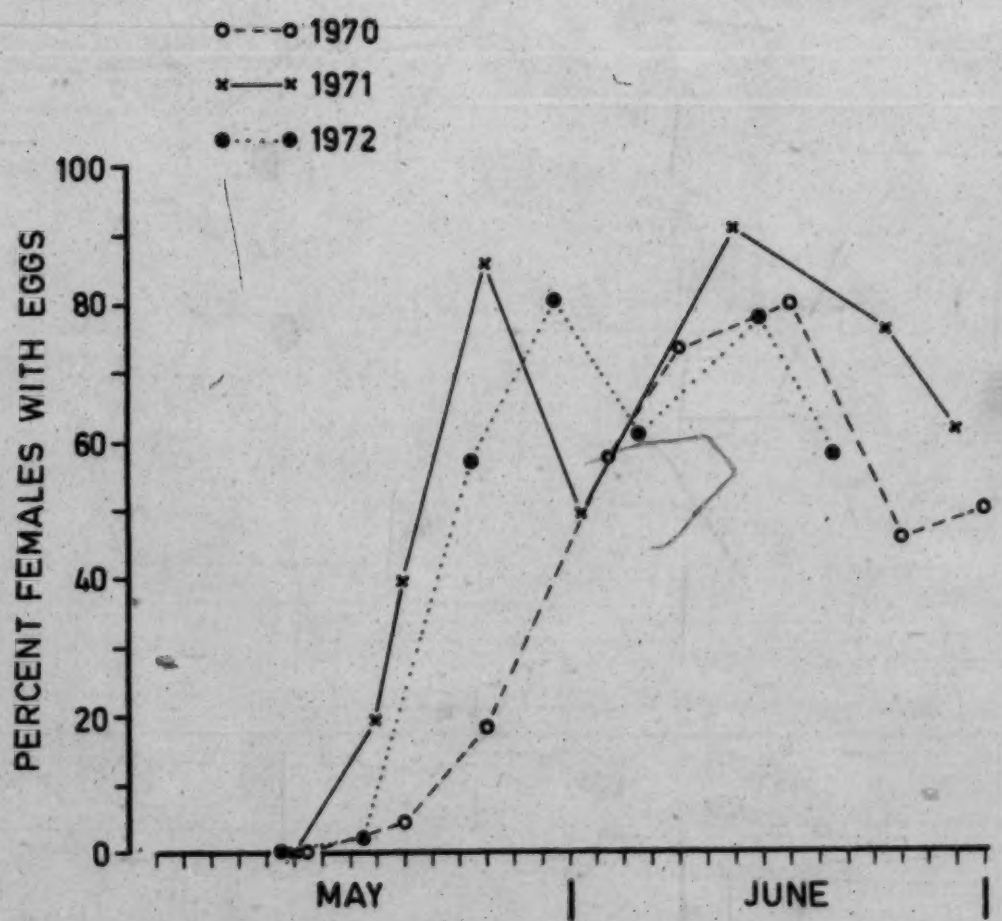
In all 3 years during April and May the sex ratio (female/male) varied around an average of 1.15, indicating a slight preponderance of females. As the population declined during the latter part of June, however, a rise in the ratio indicated preferential mortality among males. This occurred even in 1970 when mortality in both sexes was apparently greater as a result of the microsporidan epizootic (Appendix VII). The pattern is in contrast to the data obtained by White (1967), where females consistently outnumbered males, and yet declined more rapidly at the end of the life cycle.

Reproduction

As with *B. gigas*, examination of the number of eggs present in the egg sac provides a poor measure of actual fertility (clutch size) or fecundity in *B. mackini*. In each of the 3 years, females carrying eggs in the ovisac were first collected during the first week in May at lengths of 18 to 20 mm (Fig. 15). The smallest ovigerous female recorded was 16.4 mm in length.

During 1970 the percentage of females that were ovigerous increased steadily and reached single peak in mid-June; in both 1971 and 1972, however, the corresponding curves were bi-modal, with an earlier peak during the last week in May (Fig. 15). The difference in pattern may reflect the cooler temperatures during May of the first year (see Fig. 2), and it may be that a minimum temperature is required for successful breeding (Heath, 1924; Coopey, 1950). Alternatively, the high rate of infection with *Nosema* at the end of May might have been important (Appendix VII). No attempt was made to examine egg

Figure 15. Percentage of *Branchinecta mackini* females carrying eggs in the ovisac, 1970-1972.


1970
1971
1972
PERCENT FEMALES WITH EGGS
100
80
60
40
20
0
MAY
JUNE

production by *B. mackini* under controlled conditions during this study; however, White (1967) has shown that successive broods are produced at intervals of 3 to 8 days when pairs of *B. mackini* were provided with ample food at 20 C. On the basis of 10 experiments, he estimated that potential fecundity of each female was 1220 eggs. Most of White's data, however, bear little resemblance to equivalent observations obtained during this study. For example, in his culture experiments the largest clutch produced by each pair was always greater than 200, whereas ovary counts of field-caught animals in my study (see below) indicated much smaller potential clutch size. Such differences make it a dubious procedure to apply White's data to the Fleeinghorse Lake population.

As with *B. gigas* (p. 49), ovary counts were made on a number of *B. mackini* females taken at random from samples of four successive weeks during the latter half of May and the first half of June. The number of eggs in the ovaries, transformed to logarithms, and the length of the female were plotted according to date of collection in Figures 16 and 17. For each set of data, a regression line has been fitted by the least squares method to indicate, where possible, the basic trends of the results. The lines are described by the formula:

$$\log (\text{Egg No.}) = a + bl$$

where a and b are constants describing the rate of change in clutch size with length, and length (l) is expressed in millimetres. Values for a, b, and average egg number for each sample are listed in Table X.

Figure 16. Relationships between length of *Branchinecta mackini* and number of eggs in the ovaries, 1971.

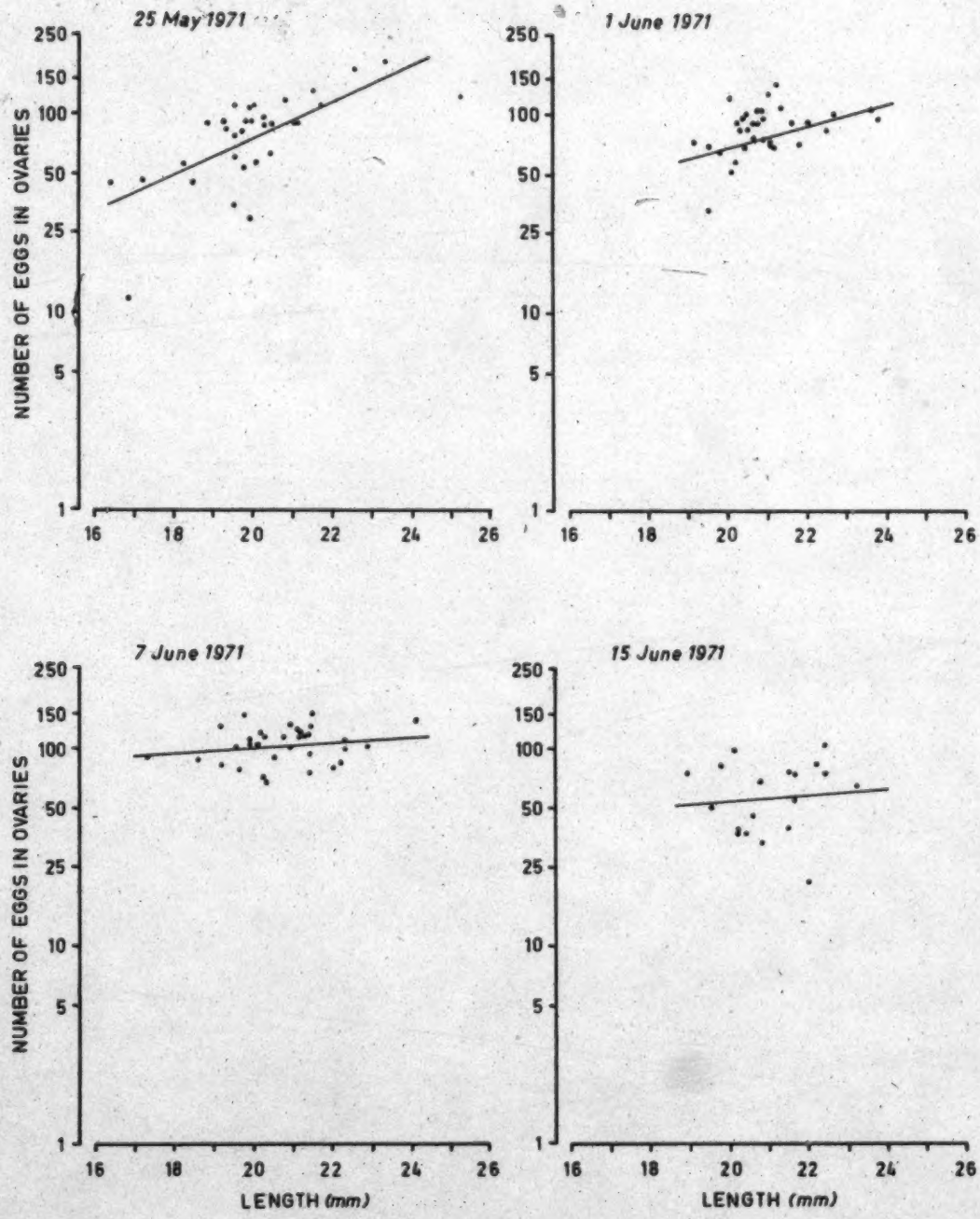

25 May 1971
1 June 1971
7 June 1971
15 June 1971
NUMBER OF EGGS IN OVARIES
LENGTH (mm)
250
150
100
50
25
10
5
1
16
18
20
22
24
26

Figure 17. Relationships between length of *Branchinecta mackini* and number of eggs in the ovaries, 1972.

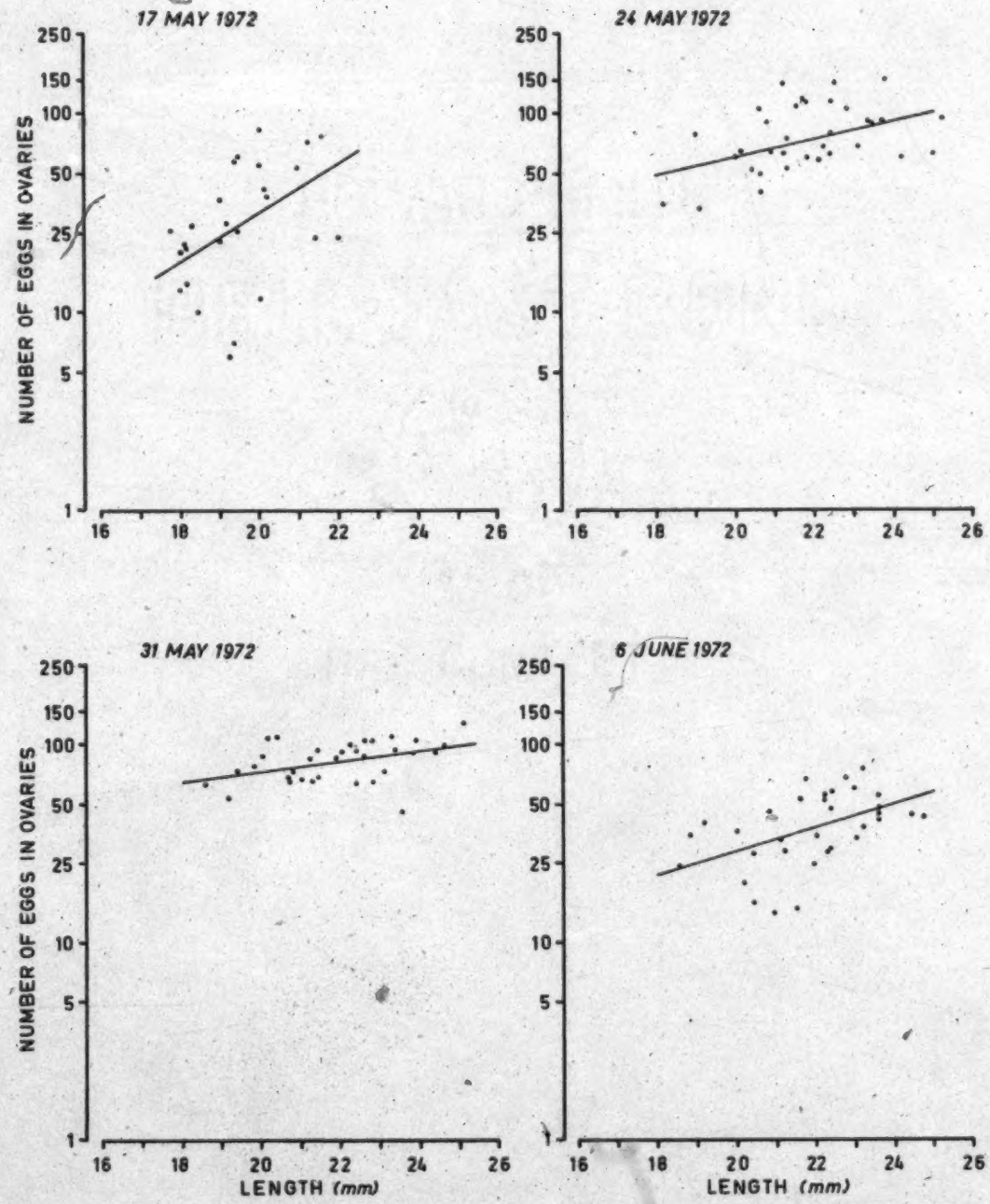

17 MAY 1972
24 MAY 1972
31 MAY 1972
6 JUNE 1972
NUMBER OF EGGS IN OVARIES
LENGTH (mm)
250
150
100
50
25
10
5
1
16
18
20
22
24
26

TABLE X. Constants for Fitted Regression Lines Relating Ovary Count to Length in *Branchinecta mackini*, and Mean Number of Eggs in Ovaries.

Year	Date	a	b	Mean No. of Eggs
1971	May 25	-0.0079	0.0942	75.3
	June 1	0.7408	0.0548	77.6
	7	1.6897	0.0158	104.1
	15	1.4489	0.0143	56.2
1972	May 17	-0.9771	0.1237	27.0
	24	0.8693	0.0462	75.3
	31	1.3476	0.0259	82.3
	June 6	0.2907	0.0585	37.3

In the earliest samples a strong correlation existed between length and ovary count (as indicated by relatively large values for b), with larger animals producing considerably more eggs than smaller ones. In subsequent weeks this relationship became progressively less evident, but at the same time, the average number of eggs in the ovaries increased. The last sample examined each year indicates rapidly declining egg production, with much greater variation than in preceding samples. Thus, while all regression coefficients were positive, indicating that maximum potential clutch size is related to length, the major determinant of egg production appears to be the age of the female. Even the strong positive correlations in each of the first samples examined may be partly explained on the basis that the larger animals were also older.

The pattern of egg production under field conditions is thus more complex than could be recognised in the results obtained for *Branchinecta gigas*. If the data regarding the percentage of females carrying eggs in 1971 and 1972 (Fig. 15) are taken at face value, however, it would appear that each female produced, on average, two broods about 15 days apart. Considering White's estimate of 3-8 days between broods under much more optimal conditions, an interval of 2 weeks in the field may not be unrealistic. With the much smaller clutch sizes recorded here, his estimated fecundity of 1220 eggs is certainly too large to apply to this population.

In contrast to the results obtained with *B. gigas* (p. 49), there is no clear indication of a change in the pattern of egg production in *B. mackini* between the two years. On the contrary, mean ovary counts

on comparable dates in 1971 and 1972 are remarkably similar (Table X).

Population Dynamics

On 19 May and 1 June 1971, weather conditions permitted the taking of a series of quantitative samples. The results obtained are given in Appendix III. The average density of *B. mackini*, calculated according to the area and mean density in each of the three basins was 181 and 89.2 per square metre on the 2 dates, respectively.

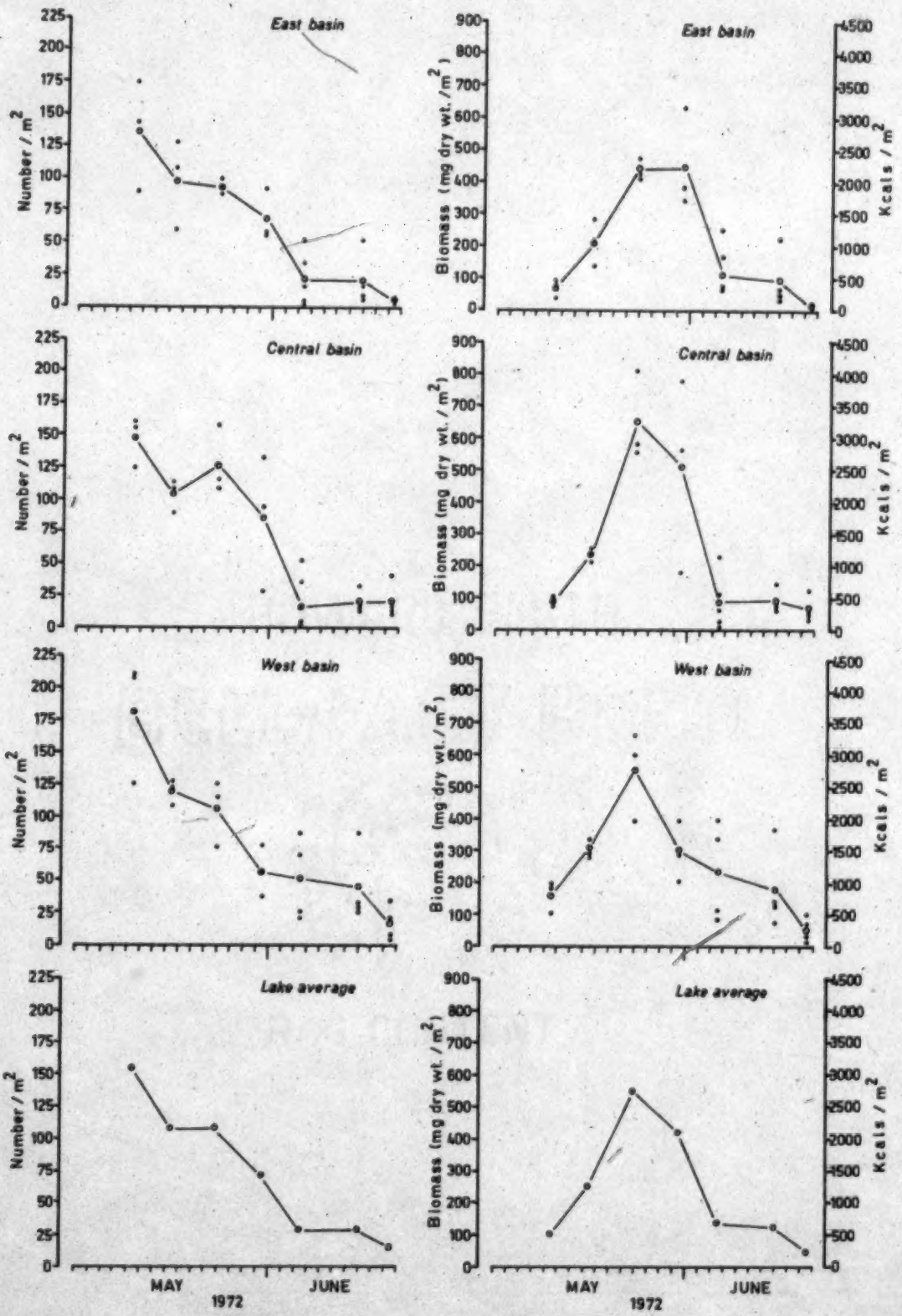
In 1972 seven sets of quantitative samples were obtained at weekly intervals. Each sample consisted of two separate hauls with a square net at points in the lake selected on the basis of random numbers. The result for each haul was recorded (Appendix IV), and the total for each sample point used to estimate the number of *B. mackini* per square metre of lake surface. Results for each of the three basins are shown in Figure 18, with an average density estimated for the whole lake on the basis of the relative area of each basin. The *B. mackini* collected in each sample were subsequently dried and weighed to obtain a measure of the population biomass per unit area. Biomass determinations in mg/m^2 are also included in Figure 18.

Decline in abundance was continuous throughout the life cycle, and followed similar patterns in all three basins. On average, mortality in the whole lake was almost 50% between 9 and 30 May, but during the second and third weeks of June, the decrease in numbers was much less rapid. Causes of this mortality cannot be ascertained with much confidence. However, although the average energy contribution of *B. mackini* to the maintenance of the *B. gigas* population is only about 50% of the latter's demand (see p. 105), this represents a consumption

Figure 18. Population numbers and biomass of *Branchinecta mackini* in Fleeinghorse Lake, 1972.

• Sample values

o Mean value of samples in each basin


East basin
Central basin
West basin
Lake average
Number / m²
Biomass (mg dry wt. / m²)
Kcals / m²
MAY
JUNE
1972

rate of between one and two *B. mackini* per day per *B. gigas*. Using the estimated abundance of *B. gigas* given in Table VII and an average consumption of 1.5 *B. mackini/B. gigas* per day, I have calculated the number of *B. mackini* that would have been consumed during each of the periods between quantitative samples, and compared these with the average decrease in abundance of *B. mackini* (Table XI). Given that many errors are involved in estimating abundance of the two species and the rate of predation of *B. gigas*, the fit is perhaps too good to be true! Nonetheless, it would seem that the *B. gigas* population is potentially capable of causing all or most of the observed mortality of *B. mackini* during May and June 1972. Certainly, *Branchinecta gigas* in Fleeinghorse Lake is a much more important influence on the life cycle and population dynamics of *B. mackini* than in the playa lake studied by Brown and Carpelan (1971).

In the absence of data on the abundance of *Diaptomus nevadensis* it is not possible to determine whether decline in numbers of *B. mackini* is the explanation for the coincident decline in *B. gigas*. There is no indication that the small fairy shrimp must be available as food for the larger, particularly as some *B. gigas* had been feeding exclusively on copepods prior to collection (Appendix V[illegible]). Furthermore, there were distinct indications that the life cycles were coming to an end in the decline of egg production by both species during June. It would appear, therefore, that these populations do exhibit senility as Moore (1963) concluded with respect to other fairy shrimp.

Probably the best measure of the presence of a species is in terms of its biomass rather than its abundance. At least when measured by

TABLE XI. Comparison of Estimated Predation Rate of *Branchinecta gigas* with Decline in Abundance of *Branchinecta mackini* in Fleeinghorse Lake, 1972.

Period	Estimated Consumption of *B. mackini*/m^2	Decline in *B. mackini* abundance/m^2
May 10 - 16	(30.6)*	39.4
16 - 23	33.6	4.72
23 - 30	30.3	30.8
30 - 5 June	18	47.8
June 5 - 14	12.3	0.5
Total	124.8	123.2

*Assuming same *B. gigas* density as 16 May.

weight some indication is given of the demand that species has on the resources of the environment, and the way in which that demand changes in time. Estimates of the dry weight of *B. mackini* per square metre obtained by weighing the quantitative samples show quite clearly that the population exerts its greatest impact on the environment during the last two weeks in May (Fig. 18). From a very low biomass originating with overwintering eggs, the weight increases rapidly through May and then declines equally rapidly as growth ceases and older members of the population die. Conversion of the biomass data into calories produces a line almost identical with that joining mean biomass values; thus, approximate caloric content of the population may be read directly from the right-hand scale in Figure 18. It is interesting to note that the greatest food supply for *B. gigas* in terms of *B. mackini* is thus made available at precisely the time that the former species exerts its greatest demand on the community (see p. 114).

LIFE CYCLE OF *DIAPTOMUS NEVADENSIS*

The co-occurrence of two species of copepod of greatly different sizes is a familiar feature of permanent or semi-permanent aquatic habitats (Hutchinson, 1951). Often such coexistence is attributed to differences in feeding habits (Cole, 1961, 1966), sometimes correlated with the inclusion of species in different subgenera (Wilson, 1958), and almost always accompanied by temporally segregated reproductive periods (Hammer and Sawchyn, 1968). The occurrence of two species of *Diaptomus* in Fleeinghorse Lake is thus almost to be expected, and their specific identity perhaps even less surprising. *Diaptomus sicilis* is a widely distributed species occurring at many different salinities, but is most frequently found in moderately saline conditions (Whittaker and Fairbanks, 1958; Reed, 1967; Anderson, 1970*b*). *Diaptomus nevadensis*, on the other hand, may be the only North American calanoid that is exclusively associated with saline waters (Wilson, 1958). The two species are greatly different in size, *D. nevadensis* females reaching 3.8 mm in length, while *D. sicilis* has a maximum size of 2 mm.

These size differences were sufficient to allow identification of both species through all nauplial and copepodid stages, and since *D. nevadensis* was of such importance in the nutrition of *Branchinecta gigas*, I felt it necessary to pursue the examination of its life cycle in some detail. In fact, very few studies have been made of the life cycles of prairie or plains copepods (Sawchyn and Hammer, 1968), and the simple community structure in Fleeinghorse Lake afforded an excellent opportunity to amend this to some extent.

Hatching

First nauplii (0.175-0.225 mm length) were collected in 1971 and 1972 as the sediments began to thaw; the range in total length is almost the same as that of egg diameter: 0.17-0.20 mm (mean 0.19 mm). Samples taken one week later apparently contained no first nauplial stages, and so it is concluded that hatching was restricted to only a few days in early spring. Perhaps similar mechanisms regulate hatching in *D. nevadensis* as in the fairy shrimp (pp. 33, 56). At all events, there is no reason to assume that uniformity of size and instar of populations in the field are the result of cannibalism, as suggested by Anderson (1970*a*).

Growth

Growth in calanoid copepods occurs through six distinct nauplial stages and five pre-adult copepodid stages, all of which are recognisable on the basis of shape or the degree of limb development, or both. In theory, increase in size is discontinuous as in other crustaceans (Teissier, 1960). Perhaps because of the flexibility of the copepod integument and the insensitivity of the method used for measurement, however, recorded lengths form a complete series, and therefore growth was treated as if it were continuous. The range of lengths observed in each developmental stage during this study is given in Table XII.

At intervals of a few days during the study periods of 1971 and 1972, plankton collections were taken and preserved, and subsequently 100 specimens from each sample were examined at random. The sex, length and developmental stage of each was recorded. The data,

TABLE XII. Range of Lengths Associated with Each Developmental Stage of *Diaptomus nevadensis* in Fleeinghorse Lake, 1971 and 1972.

Stage		Sex	Length Range (mm)
Nauplius	1		0.175-0.225
	2		0.225-0.300
	3		0.325-0.380
	4		0.390-0.475
	5		0.475-0.625
	6		0.625-0.825
Copepodid	I		0.84 - 1.25
	II		1.25 - 1.64
	III		1.65 - 1.85
	IV	M	1.90 - 2.10
	IV	F	1.90 - 2.10
	V	M	2.20 - 2.60
	V	F	2.20 - 2.70
Adult		M	2.70 - 3.50
		F	2.75 - 3.85

DONATED BELFAST BOND

reduced to show mean length, standard deviation and range on each sample date, are presented in Figures 19 and 20. Sex could only be determined in adults and copepodid stages IV and V (Table XII), and therefore the curves based on earlier stages are identical for both sexes. Following hatching, growth was slow at first but proceeded at an increasingly rapid rate until at the end of May the majority of individuals were in the last copepodid stage or were already adult. The growth pattern described a sigmoid curve which, as in the fairy shrimp, is best represented by the logistic formula (Appendix II). The fit of the empirical and derived curves was very close in 1971 (Fig. 19), but considerably less so in 1972 (Fig. 20). Furthermore, both the maximum rates of growth (0.074 mm/day) and the asymptotes approached in 1972 (k in Fig. 20) were much less than in the previous year (0.147 mm/day and k in Fig. 19). There are indications that the average length of both sexes was still increasing when the last samples were taken on June 19, 1972. These patterns are thus similar to those obtained with *Branchinecta gigas*, in which both asymptotes and maximum growth rates were lower in 1972 than in 1971; but are in contrast to those of *B. mackini*. As indicated with respect to *B. gigas*' growth patterns, I assume that these differences reflect changes in some quality or qualities of the environment. Unfortunately, ancillary aspects of this study provide no indication of what the important environmental parameters might be.

Length-Weight Relationships

Since *D. nevadensis* is such an important food item for the giant

Figure 19. Growth of *Diaptomus nevadensis* in Fleeinghorse Lake, 1971.

——— Line joining sample means (·)

- - - - Fitted logistic curve (see text)

vertical rectangle - mean ± 1 s.d.

vertical line - range of sizes

a, b Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve

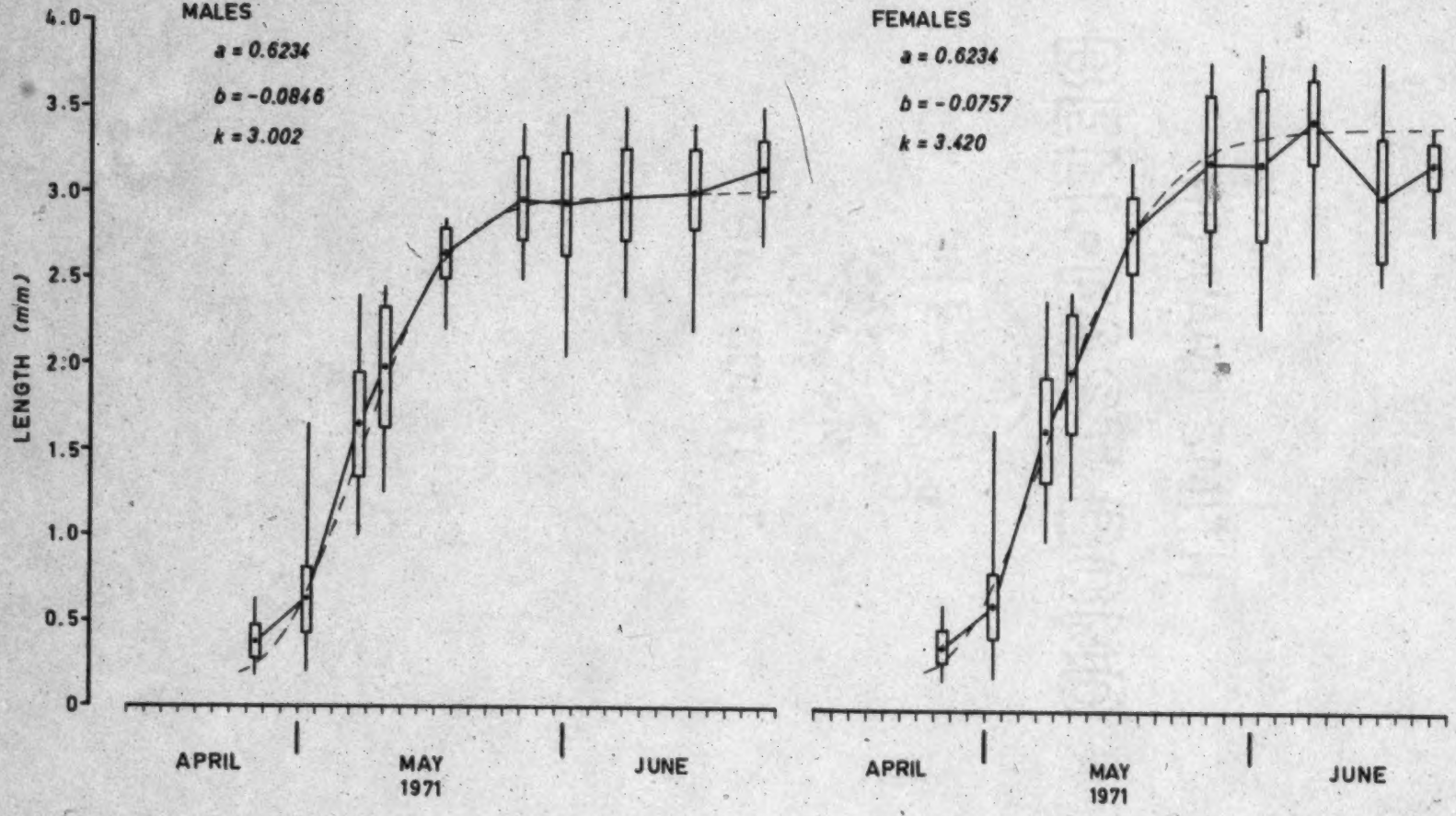

MALES
a = 0.6234
b = -0.0846
k = 3.002
FEMALES
a = 0.6234
b = -0.0757
k = 3.420
LENGTH (mm)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
APRIL
MAY
1971
JUNE
APRIL
MAY
1971
JUNE

Figure 20. Growth of *Diaptomus nevadensis* in Fleeinghorse Lake, 1972.

——— Line joining sample means (•)

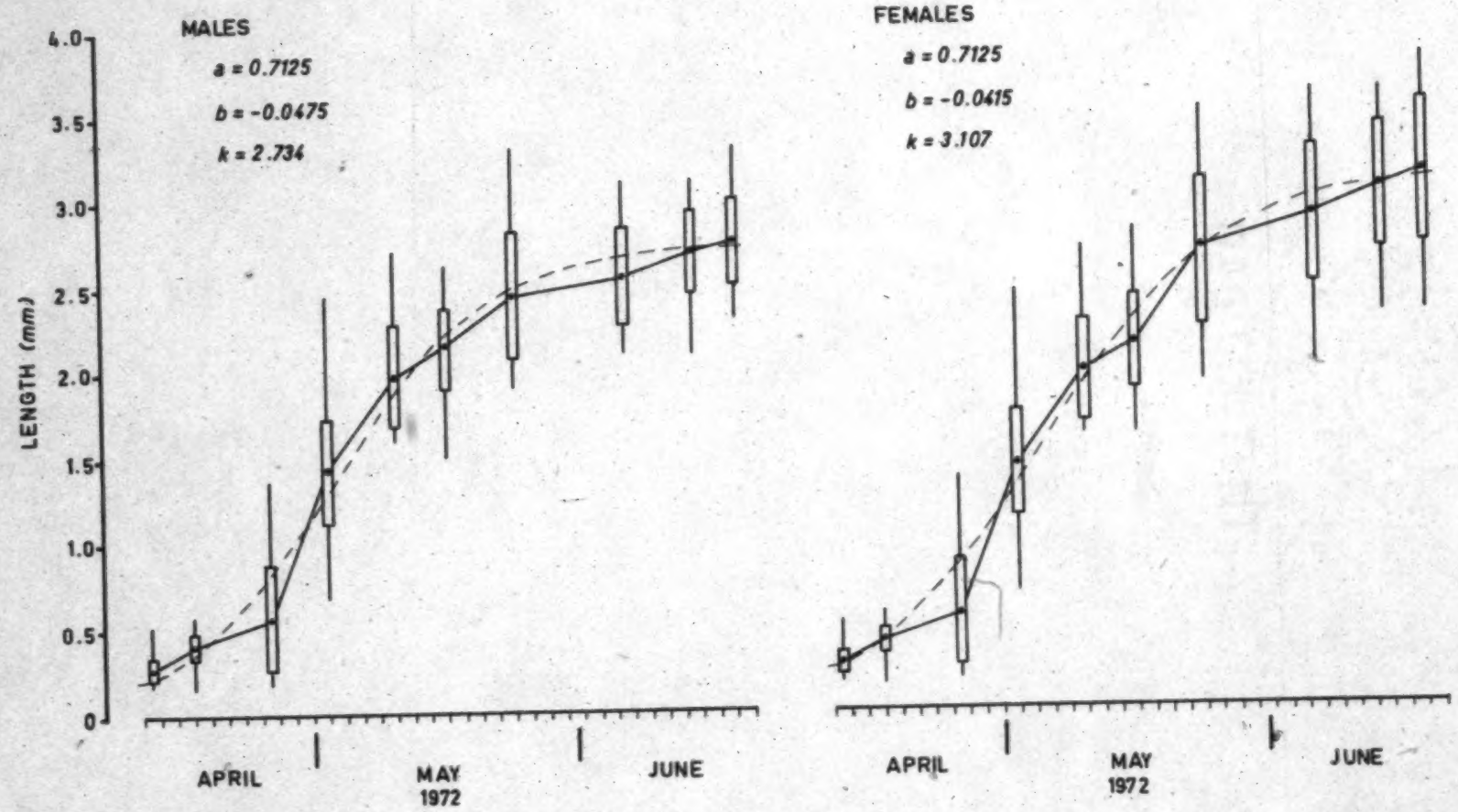
- - - - Fitted logistic curve (see text)

verticle rectangle - mean ± 1 s.d.

vertical line - range of sizes

a, b Constants of fitted logistic curve (see text)

k Asymptote of fitted logistic curve


MALES
a = 0.7125
b = -0.0475
k = 2.734
FEMALES
a = 0.7125
b = -0.0415
k = 3.107
LENGTH (mm)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
APRIL
MAY
1972
JUNE
APRIL
MAY
1972
JUNE

fairy shrimp, it was necessary to obtain data that would allow conversion of length measurements into terms of biomass. Technical difficulties precluded determination of wet weight, but a large number of specimens were measured, classified according to sex and developmental stage, dried and weighed. As expected, the relationship between length and weight is an exponential one, which becomes a straight line when transformed to logarithmic form (Fig. 21). Although the male and female regression lines lie close together, their respective coefficients (3.39 and 3.61) are highly significantly different ($p < 0.001$; 103 df). Juveniles exhibit a totally different weight-length relationship (b = 1.79) from that of adults and late copepodid stages. The change in allometry occurs between copepodid III and IV—when the newly-formed fifth legs show the first external signs of sexual differences.

Reproduction

Although sexually mature *D. nevadensis* were present by the beginning of June in both years, only two ovigerous females were found out of 503 examined during the last 2 weeks of June 1971, and only one out of 250 in the same period in 1972. Occasional visits during the summer and autumn of both years indicated that the breeding period extends throughout the months of July to October. The data are insufficient to characterise this breeding period more exactly. On 22 October 1972, however, a plankton haul taken from the central basin contained large numbers of *D. nevadensis*, all of which were mature. Egg 'floats' from ten ovigerous females were examined and the number of eggs counted. The results are given in Table XIII and indicate clearly that clutch size tends to increase with the size of the female.

Figure 21. Relationships between length (l) and dry weight (ω) in *Diaptomus nevadensis*.

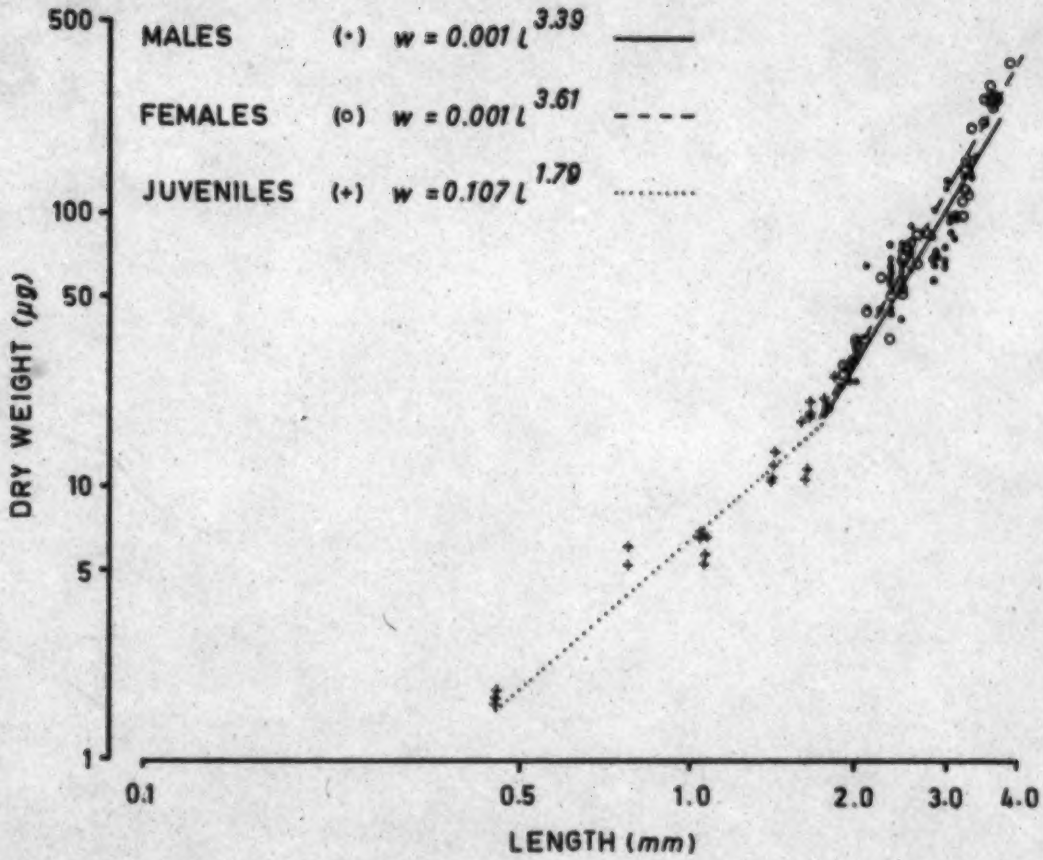

MALES (•) w = 0.001 l 3.39
FEMALES (o) w = 0.001 l 3.61
JUVENILES (+) w = 0.107 l 1.79
DRY WEIGHT (µg)
500
100
50
10
5
1
0.1
0.5
1.0
2.0
3.0
4.0
LENGTH (mm)

TABLE XIII. Clutch Size in *Diaptomus nevadensis* from Fleeinghorse Lake, 22 October 1972.

Length (mm)	No. Eggs in 'Float'
2.8	50
2.8	63
2.9	54
3.0	81
3.1	62
3.2	101
3.2	112
3.4	95
3.4	116
3.5	129
	Mean No.: 86.3

Of 10 males dissected, all were found to contain two spermatophores, one of which was usually more fully developed than the other. The examination was prompted by the finding of one female that carried three spermatophores all inserted into the gonopore. It is apparent, therefore, that a female may copulate with more than one male at the onset of each brood.

* * * * *

Study of the life cycle of *Diaptomus nevadensis* was instigated as a result of its obvious importance to the energetics and dynamics of the giant fairy shrimp. Unfortunately, time did not permit any determinations of biomass, although observations in the field suggest that this is quite substantial. Its large size, limited hatching period, long life and possibly predatory nature make it a very interesting and suitable species for the further study of calanoid biology.

AN ENERGY BUDGET FOR *BRANCHINECTA GIGAS*

The main objective of this study was to obtain, under field conditions, sufficient information to construct an individual energy budget for the giant fairy shrimp. The major pathways along which energy flows within an organism are related according to the following equation:

$$C = P + E_x + R + F + U$$

where C = the energy ingested by the individual; P = the energy involved in growth (P_g) and production of gametes (P_r); E_x = the losses through ecdysis; R = metabolic or respiratory loss; F = energy passed through as faeces, and U = energy lost through non-faecal excretion of all kinds. The equation is essentially that used by Richman (1958) converted to the conventional symbols recommended by Petrusewicz (1967) and Ricker (1968). Ideally, each component of the equation should be assessed independently, and at all major periods of the life cycle. This has so far proved impossible.

In many cases, the value of C has been derived from the equation itself rather than by independent determination, and this removes the best internal check of the consistency of those measurements obtained (Hughes, 1970). Frequently, the equation is simplified by omitting consideration of the loss of energy through various forms of non-faecal excretion (U)—predominantly the output of urine. Because of difficulties of measuring rates of urinary output in the field, I decided to omit this parameter also. Recently, however, Hargrave (1971) has shown that energy lost by this route is of considerable significance

in the total budget of the amphipod *Hyalella azteca*.

Energy of Growth (P_g)

The pattern of growth in length of *Branchinecta gigas* and the exponential relationships between weight and length have been described above. At the outset it was assumed that the caloric value of body tissues might change during the life cycle as the relative quantities of protein, carbohydrates and fats varied. Such changes have been well documented in insects, where the quantities of lipid storage products increase as the stage of diapause or pupation is approached (e.g. Wiegert, 1965; Gyllenberg, 1969). Similar, if less predictable, variations have been recorded in many fresh-water crustaceans (Wissing and Hasler, 1968, 1971; Moshiri and Cummins, 1969; Green, 1971; Schindler *et al.*. 1971; Solomon and Brafield, 1972; Teraguchi *et al.*, 1972).

Accordingly, *B. gigas* of varying sizes were used in determinations of caloric value. The results are presented in Figure 22. Except for the three specimens indicated, females were selected that did not carry eggs in the ovisac; correspondingly, some of the variation in caloric value may be attributed to the varying maturity of the shell glands and the number and maturity of eggs in the ovaries.

A correction was made for ash content on the basis of a series of tests using *B. mackini* (Table XIV). Fourteen mixed samples of *B. mackini* (without ovigerous females) were dried at 50 C for 72 hours, weighed and incinerated in open crucibles at 520 C for 12 hours. The average ash content of 17.17% is somewhat higher than that for 2 mm *Artemia* (Paffenhöfer, 1967), but nearly twice the value given by Bernice (1972*a*) for *Streptocephalus dichotomus* and *Branchinella*

Figure 22. Caloric values of *Branchinecta gigas*.

Mean caloric value of eggs indicated by arrow.

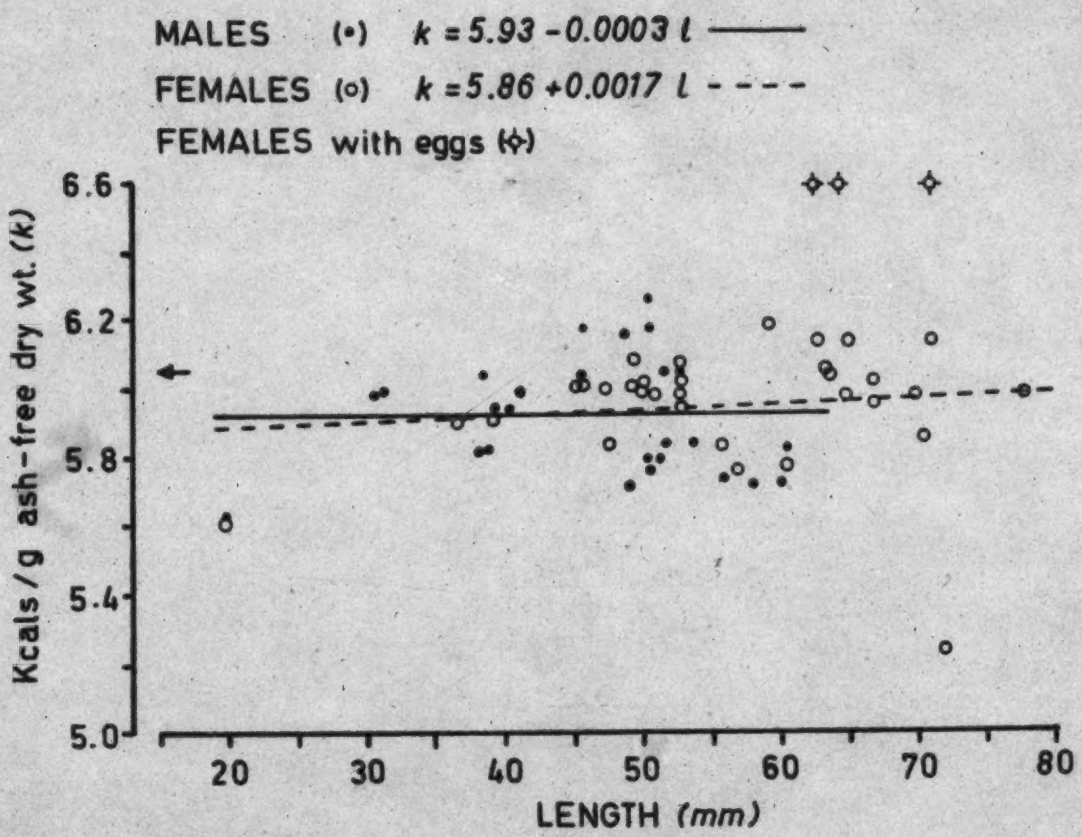

MALES (•) k = 5.93 - 0.0003 l
FEMALES (o) k = 5.86 + 0.0017 l
FEMALES with eggs (◊)
Kcals / g ash-free dry wt. (k)
6.6
6.2
5.8
5.4
5.0
20
30
40
50
60
70
80
LENGTH (mm)

TABLE XIV. Ash Content of *Branchinecta mackini*.

Test No.	Dry wt (g)	Ash wt (g)	% Ash
1	1.9117	0.3310	17.31
2	1.4789	0.2530	17.11
3	2.1833	0.3788	17.30
4	2.4832	0.4135	16.65
5	2.8073	0.4751	16.92
6	3.5278	0.6061	17.18
7	2.3786	0.4137	17.39
8	2.9648	0.5134	17.32
9	3.6669	0.6494	17.71
10	2.5881	0.4399	17.00
11	2.3860	0.4128	17.30
12	3.4484	0.5897	17.10
13	3.0612	0.5173	16.90
14	3.6741	0.6319	17.20
		Mean Ash %:	17.17

kugenumaensis. The difference almost certainly lies in technique: Bernice burned the animals at 700 C, at which temperature breakdown of carbonates would have been substantial (Paine, 1966; Cummins and Wuycheck, 1971).

There is clearly no consistent variation in caloric value with length in *B. gigas* over the range covered (Fig. 22). Furthermore, with the exclusion of ovigerous females, there is no significant difference between the male and female regression lines ($p > 0.5$; 54 df), nor between their respective means—5.918 and 5.946 Kcals/g ash-free dry weight. Two determinations only were made on eggs collected from females kept alive in the laboratory; the average caloric value of 6.056 Kcals/g is indicated on the graph by an arrow. Females with full ovisacs, however, had an average caloric value of 6.585 Kcals/g ash-free dry weight.

With these results and the data available on growth rates and length-weight relationships it is possible to calculate the amount of energy represented by biomass accumulation during an individual life cycle (P_g). For an average 1972 male attaining 47.7 mm in length (see Fig. 7) 165 calories were accumulated as body tissue, whereas a 60.6 mm non-ovigerous female (see Fig. 7) accumulated 297 calories.

Moulting Loss (E_x)

Throughout this study, attempts have been made both to witness moulting and to collect shed integuments for examination and calorimetry, but without success. Although moulting certainly took place in animals kept in non-sterile cultures, the fragments of skin always disappeared within 24 hours; only the heavily-tanned mandibles were

more resistant. During respiration experiments, however, the remains of shed integuments were frequently seen, but could not be collected because the continuous swimming of the captive animal had resulted in considerable fragmentation. Thus, no independent measurement could be made of ecdysis, or the energy losses associated with it.

Few studies of fairy shrimp have included enumeration of the number of moults that occur during the life cycle. Recently, however, Bernice (1972*d*) concluded that there were 15 pre-adult developmental stages in *Streptocephalus dichotomus*, each stage being distinguishable on morphological criteria, and successive stages probably separated by ecdysis. Khmeleva (1967), on the other hand, determined that *Artemia salina* moults 25 to 27 times in a life cycle of 130 days, at each moult casting off a skin that is 5% of the dry weight of the animal. If it is assumed that adult *Branchinecta gigas* also moult during the 20-25 day period following maturation (see Fig. 7), an estimate of 20 moults during the whole life cycle seems appropriate. The total weight of exoskeleton lost in 20 moults would be 16.06 mg for a male and 31.51 mg for a female.

In *Daphnia*, the cuticle is composed primarily of chitin, with 12% ash and a caloric value of 5.753 cals/mg ash-free dry weight (Wissing and Hasler, 1968). Adopting these values, the energy loss associated with 20 moults in *B. gigas* may be calculated as 81.31 calories for an average 1972 male and 159.52 calories for an average female. In each case, this quantity amounts to half of the energy deposited in body tissue; for a somewhat different type of life cycle, Khmeleva (1967) estimated that *Artemia* lost as much energy in moulting as it deposited

in growth. The above estimates for the rapidly-growing giant fairy shrimp may therefore be close to actuality. By way of comparison, estimates of energy losses in *B. gigas* calculated on the assumption of 15 and 25 moults during the life cycle amount to 72.73 and 113.44 calories respectively for males, and 121.47 and 201.23 calories respectively for females.

Egg Production (P_r)

Various methods were tried during this study to determine the amount of energy used by a female *B. gigas* in the production of eggs. None of these were successful. In *B. mackini*, however, there was some evidence to suggest that two broods were produced, on average, during 1972 (Fig. 15). If the same is assumed to be true of *B. gigas*, with a mean ovary content of 230 eggs (Fig. 10), approximate fecundity in that year would have been 460 eggs per female. Each egg weighs an average of 40.4 µg and has an average caloric value of 6.056 cals/mg; thus the amount of energy represented by 460 eggs would be 112.5 calories.

Metabolic Loss (R)

During 1971 and 1972 individuals were enclosed in sealed containers with boiled lake water of known oxygen concentration and immersed in the lake for 24 hours. At the end of this period, the oxygen concentration was determined again, and the difference considered to be a measure of the daily oxygen consumption.

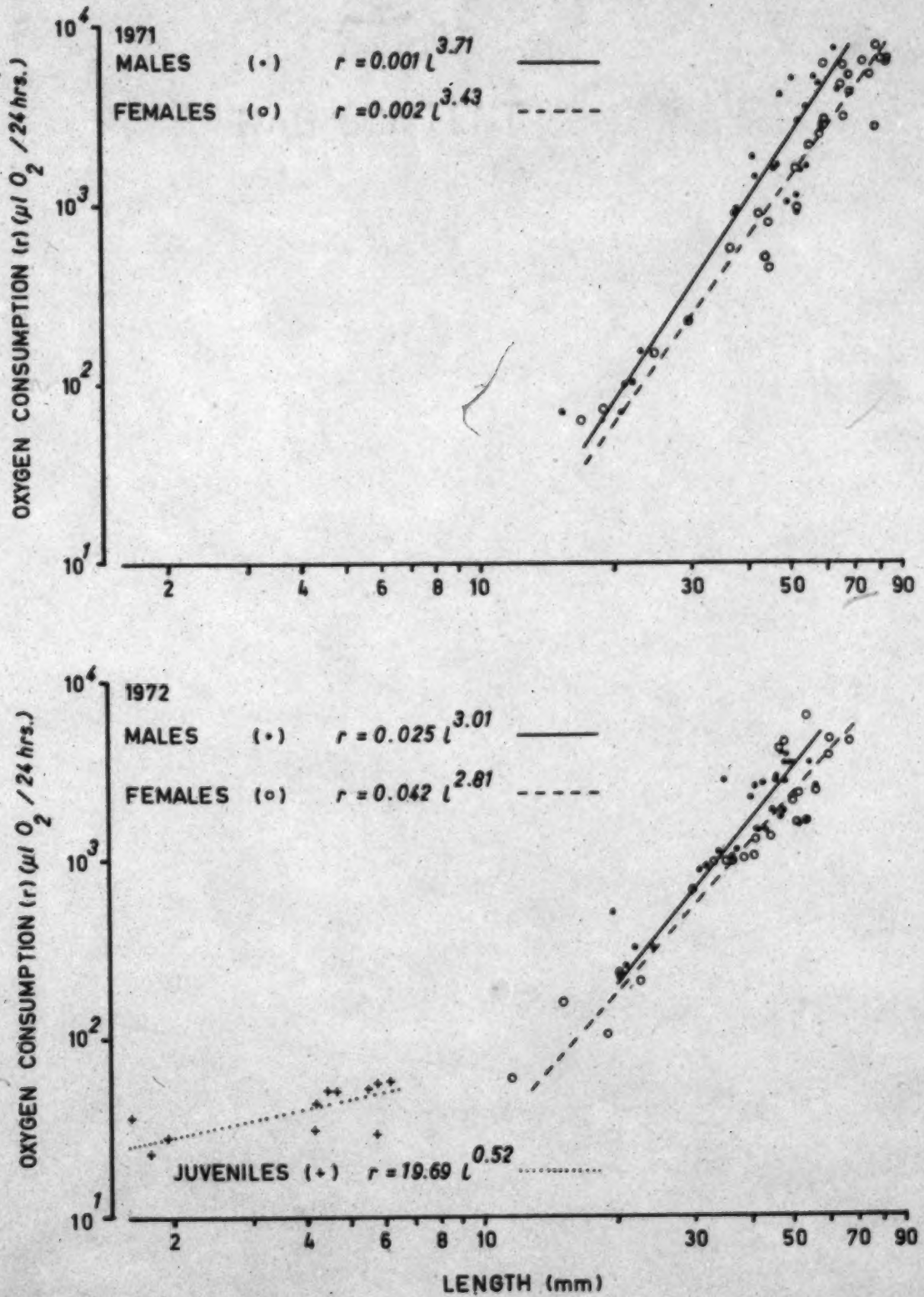
As indicated in the original description of methods (p. 9) the closed bottle technique is subject to important sources of error.

Perhaps the most significant in the present context is the effect of oxygen concentration on respiratory rate: in many crustaceans, the rate of oxygen consumption begins to decline at 50% saturation, and is depressed more rapidly as saturation falls even lower (Wolvekamp and Waterman, 1960). In the present study, particularly when the *B. gigas* were large and water temperatures high, oxygen saturation at the end of an experiment was sometimes below 10%. The magnitude of this error cannot be assessed without a laboratory investigation of the effect of varying oxygen concentration upon respiratory rate in *B. gigas*; it could not be avoided if determinations were to be made over 24 hours at lake temperatures.

The results of weekly oxygen consumption experiments during the two years are shown in Figure 23, with both axes in logarithmic form. Conventionally, measurements of oxygen consumption are reported in relation to dry weight rather than length. In this study, however, I was concerned with measuring metabolic losses directly under the conditions of varying light and temperature that occurred in the natural habitat; hence, even a weight-specific expression of metabolic rate could not be compared with constant temperature results obtained with other species in the laboratory (e.g. Gilchrist, 1956). For these reasons, and for the convenience of expressing all variables in the same units, oxygen consumption (r) is presented in terms of body length (l). Regression lines have been fitted to the data and the arithmetic formula for each is indicated on the appropriate graph.

It is evident from these results that males consume more oxygen

Figure 23. Oxygen consumption (r) of *Branchinecta gigas* in Fleeinghorse Lake, 1971 and 1972.


1971
MALES (•) r = 0.001 l^3.71
FEMALES (○) r = 0.002 l^3.43
1972
MALES (•) r = 0.025 l^3.01
FEMALES (○) r = 0.042 l^2.81
JUVENILES (+) r = 19.69 l^0.52
OXYGEN CONSUMPTION (r) (µl O2 / 24 hrs.)
LENGTH (mm)
10^4
10^3
10^2
10^1
2
4
6
8
10
30
50
70
90

than females under equivalent conditions, and that this disparity becomes greater with increasing size. In 1971, for example, a 20 mm male consumed 31.4% more oxygen than an equal sized female, whereas at 50 mm the difference was 68.6%. The average difference over this range was 51.3%. During 1972, however, the differences were considerably less: *viz.* 11.1, 34.4 and 23.7% respectively. Differences in the latter year are a little greater than sexual differences in dry weight, which average 16 per cent. The great difference between male and female oxygen consumption rates in 1971 is inexplicable on the basis of present data.

Sexual differences in metabolic rates of arthropods are well known (e.g. MacArthur and Baillie, 1929; Knight and Gaufin, 1966). Males usually consume more than females, although exceptions are to be found (e.g. Kucera, 1934). In the present case, however, despite the apparent differences in respiration rates of males and females, the variance of the data is so high that neither the means ($p > 0.1$) nor the regression coefficients (1971 $p > 0.1$, 48 df; 1972 $p > 0.1$, 50 df) are significantly different. This corresponds with the fact that dry weights are also not significantly different.

Oxygen consumption results for each sex showed highly significant differences between years. On average, over the range from 20 to 50 mm length, males consumed 67% more oxygen in 1972 than in 1971 ($p < 0.001$, 50 df), and females 110% more ($p < 0.001$, 48 df). Considering the conditions under which these experiments were conducted, such changes between years are probably to be expected, and may well reflect basic differences in environmental conditions or mode of life.

Only a few values were obtained for juveniles during 1972. The very different relationship indicated by an exponent of 0.52 is partly a function of low temperatures at the time of measurement (April), but also recalls the different allometric relationship between weight and length for sizes below 7 millimetres.

On the basis of these data, the total metabolic loss of energy (R) may be calculated for males and females for the majority of the life cycle in 1972. In order to do so, it is necessary to assume a value for the caloric equivalent of the oxygen consumed. This is usually done by reference to the major substrate utilised, as indicated by the respiratory quotient, but in this study no direct determination of R. Q. was made. The only studies of the respiratory quotient in the Anostraca appear to be those on *Artemia salina*, and indicate that it varies around 0.82 (Wolvekamp and Waterman, 1960), but changes according to both stage of development (von Hentig, 1971) and temperature (Grainger, 1956). The substrates involved were assumed to be a mixture of carbohydrates and lipids, with the latter providing the main energy reserve. In view of the apparently high lipid content of *B. mackini* and *D. nevadensis* and the rapid growth of *B. gigas*, an R. Q. of 0.8 is probably a suitable choice here also, particularly during the period of major growth. This corresponds to an oxycaloric equivalent of 4.85 cals/ml (Wiegert, 1964; Ito, 1964). In fact, over the whole range of R. Q. values, the oxycaloric value varies only by 7% (Richman, 1958), so the maximum error involved in thus adopting an R. Q. value is not very great in comparison with other errors involved in this aspect of the budget. Using these values, the daily energy loss was calculated

for individuals following the theoretical logistic curves shown in Figure 7. By integration, the total metabolic loss for an 'average' male in 1972 attaining 47.7 mm and surviving until June 15 was estimated at 427.4 calories; for an average 1972 female reaching 60.6 mm the corresponding loss was 643.0 calories.

Urinary Loss (U)

As indicated above, rates of urine output could not be measured directly. Recently, however, Bernice (1972*c*) determined that total nitrogen excretion by the fairy shrimp *Streptocephalus dichotomus* amounted to 1.52 (± 0.13) and 1.39 (± 0.19) mg N/g wet weight per day for males and females respectively, at their 'optimum' temperature (30 C). The majority of this nitrogen (75%) was in the form of ammonia as it is in most fresh-water crustaceans (Parry, 1960), and the values fall within the range reported by Conover and Corner (1968) for a variety of boreal marine copepods. Using these estimates, and a caloric equivalent for ammonia of 4.06 cals/mg (Brafield and Solomon, 1972), a first order approximation may be made of urinary losses. Thus, a minimal value of U for an average male surviving to June 15 would be 100.8 (± 8.6) calories, and for a female, 190.4 (± 25.7) calories. These estimates must be considered minimal because this species lives on a diet that is high in protein and lipids, and therefore the remaining 25% of urinary output would likely consist of more complex products with greater quantities of energy.

Faecal Loss (F)

Non-assimilated material from the gut is extruded within a thin

peritrophic membrane that consists of chitinous microfibrils in which proteins and mucopolysaccharides are localised (Georgi, 1969). Thus, faecal pellets consist of both assimilated and non-assimilated energy. In *Artemia* (Reeve, 1963*c*) and *Branchinecta*, however, the membrane is extremely fine and easily broken, so that collection of faeces for examination and calorimetry is a delicate operation. Attempts were made to collect pellets from *B. gigas* confined in various containers, but their continuous swimming usually broke up and dispersed the pellets produced and, as a result, no separate estimate of F could be made.

Energy Ingested (C)

Under conditions of captivity *B. gigas* will apparently eat any live animal food that it is able to catch between the swimming legs. The method of prey capture has been described by White *et al.* (1969) and the limb modifications associated with feeding by Fryer (1966). In the field, however, the variety of potential prey is limited, and it was necessary, therefore, to examine the intestinal contents of as many field-caught animals as possible to determine the main items of the diet. The results of these analyses are tabulated in Appendix V.

During the first few days of life the nauplius and probably the first metanauplius do not feed, but survive on the large quantities of yolk stored within the body. During the first feeding phase (2 to 5 mm), the gut contains completely undifferentiated material ('feinde-tritus', cf Hutchinson, 1937) that looks exactly like the sediment particles suspended in the lake water; occasional spines and other fragments were probably obtained by scraping the mud bottom as

described by Tasch (1970). Active predation begins at lengths of 7-10 mm as the legs become sufficiently developed to enable prey to be clasped and moved to the mouth. During the rest of the life cycle, *B. gigas* appears to subsist on a mixed diet of *Branchinecta mackini* and *Diaptomus nevadensis*, with some *D. sicilis* and *Daphnia similis* (Appendix V). Results of calorimetric determinations of the first two species are given in Table XV.

The extreme turbidity of the lake, the small eyes, and modified feeding behaviour all indicated that *B. gigas* probably obtained its food by filtering prey from the water, rather than pursuing it by sight. Thus, the rate and type of prey capture was primarily determined by such factors as prey size, agility, and abundance. Nevertheless, analysis of gut contents showed that food consisted of any combination of the two main items, from 100% *B. mackini* to 100% *D. nevadensis*. For *B. gigas* feeding on a combination of these two species, however, it was obvious that the majority of the energy derived came from ingested *B. mackini*. When the numbers of each prey species present in the gut were converted to energy units (based upon the mean size of each species on the day of capture, and their caloric value, Table XV), a correlation was found between the size of the predator and the percentage of its energy intake derived from *B. mackini*. The results are shown in the upper graph of Figure 24. Despite the considerable scatter of the data, a trend is evident whereby at larger predator sizes, the percentage of energy derived from *B. mackini* also increased. Although not shown in this figure, the majority of individuals whose gut contents consisted solely of *Diaptomus* were small in

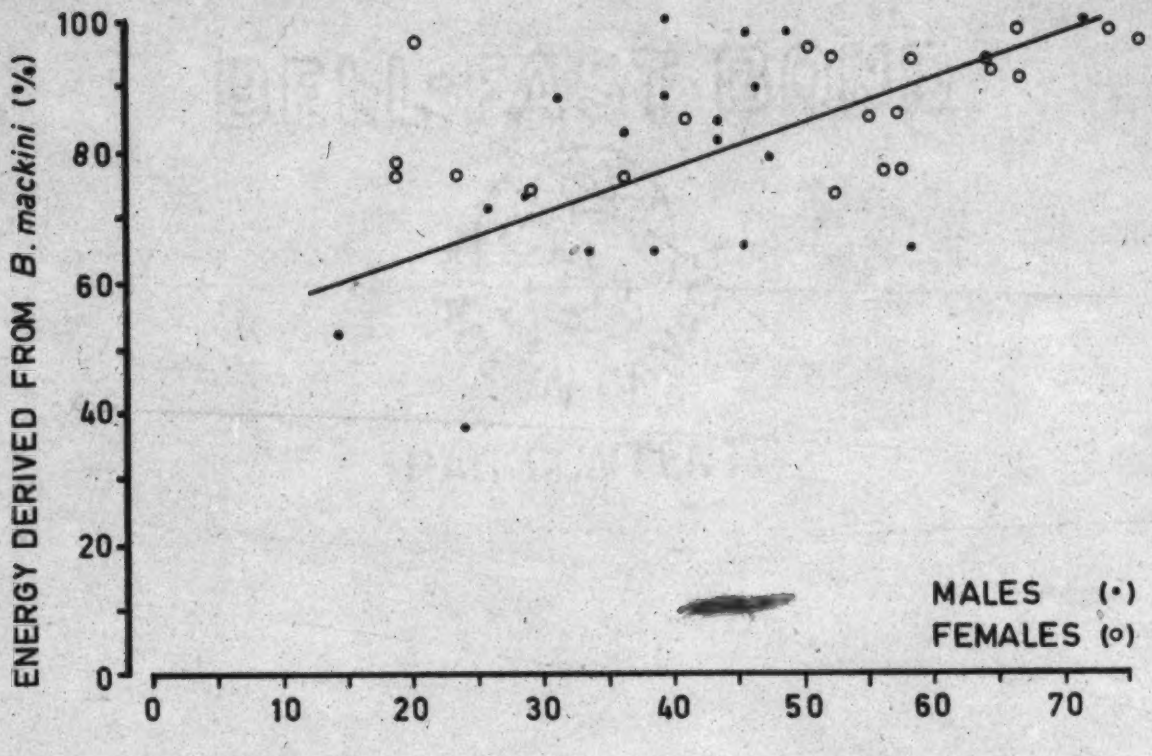
TABLE XV. Caloric Values of *Branchinecta mackini* and *Diaptomus nevadensis*, Fleeinghorse Lake.

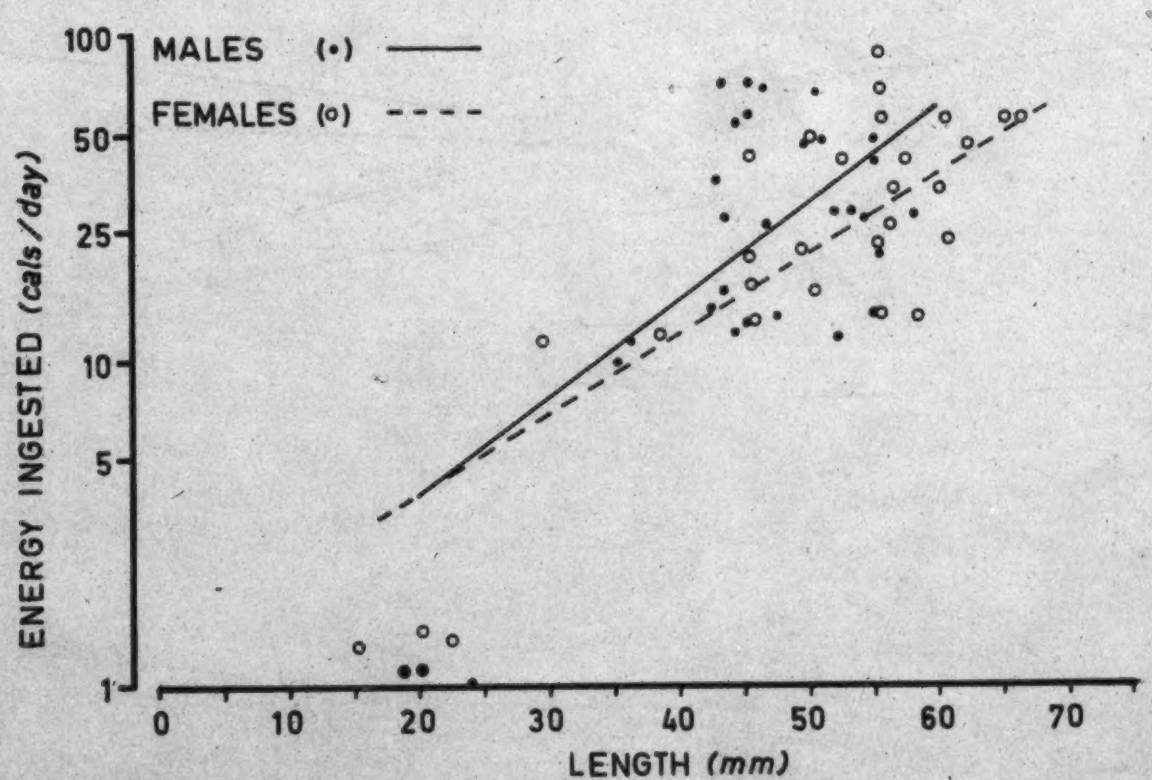
Species	Sex	No. Determinations	Kcals/g dry wt (Mean ± s.d.)
B. mackini	M	14	5.751 ± 0.253
	F	13	5.774 ± 0.270
D. nevadensis		6	5.739 ± 0.183

Figure 24. Energy intake relations of *Branchinecta gigas*, 1972.

Upper graph: Percentage of energy derived from *B. mackini* as a function of length of *B. gigas*.

Lower graph: Energy consumed during feeding experiments as a function of length of *B. gigas*.


ENERGY DERIVED FROM B. mackini (%)
100
80
60
40
20
0
0
10
20
30
40
50
60
70
MALES (•)
FEMALES (o)


ENERGY INGESTED (cals/day)
100
50
25
10
5
1
MALES (•)
FEMALES (o)
0
10
20
30
40
50
60
70
LENGTH (mm)

size, and those feeding exclusively on *B. mackini* were usually larger. The line shown was fitted by the least squares method, and is described by the equation:

$$\text{Percent of energy} = 50.17 + 0.70l.$$

It seems likely, therefore, that a change occurs in the pattern of energy flow into the *B. gigas* population during the life cycle. Since attempts to measure feeding rate using *Diaptomus* were unsuccessful, it was decided that measurements of predation rate on *B. mackini* alone would provide an index that could be adjusted to give an estimate of total ingestion rate. This is probably appropriate if the assumptions underlying the account of prey selection given above are valid: i.e. that the presence of one prey species does not materially affect the probability that a member of the other species would be seized—except, of course, at the moment of capture. Accordingly, a series of feeding experiments using *Branchinecta mackini* as the only food were set up as described on Page 11. The results are tabulated in Appendix VI.

From the number of *B. mackini* consumed during 24 hours, their mean weight and caloric value, the amount of energy ingested during each experiment was calculated, and plotted on a logarithmic scale against the length of the *B. gigas* used. The results are shown in the lower graph of Figure 24, with regression lines fitted by a least squares method. Equations for the lines are as follows:

$$\text{Males: } \log(\text{cals. ingested}) = 0.0298\,l - 0.0162$$

$$\text{Females: } \log(\text{cals. ingested}) = 0.0246\,l - 0.0993.$$

As a description of the energy consumed by *Branchinecta gigas* during its life cycle, the data are clearly inadequate. There is very wide scatter of the points partly because one unit of food (i.e. one *B. mackini*) represents up to 19 calories, depending on size, and also because most experiments utilised large *B. gigas* specimens, and hence the results are aggregated toward the high end of the scale. Nevertheless, the data are the only ones available, and have the additional merit that for large sizes of *B. gigas*, the estimated energy consumed is sufficient to account for the calculated quantities of energy lost in respiration, moulting and urine output and accumulated in growth. Therefore, *in lieu* of more satisfying determinations, results of these feeding experiments have been used to provide a tentative account of the overall partitioning of the energy budget for an individual *Branchinecta gigas*.

Using the data of both graphs of Figure 24, as summarised by the fitted regression lines, and the calculated growth curves for 1972, the total energy consumed by an average male and female from 30 April until 15 June 1972 was estimated at 1088 and 1452 calories, respectively.

Cumulative Energy Budget

Of the various parameters involved in the energy budget of an individual, measurements of varying accuracy were obtained for the three most important ones: ingestion, growth and metabolic losses. In addition, sufficient data were available in the literature to make reasonable approximations of energy losses involved in ecdysis and non-faecal excretion. Few of the measurements obtained during this study involved animals smaller than 20 mm in length, and in view of

the extensive changes in the species' biology occurring at lengths of 7-10 mm, extension of the results to cover smaller individuals would be unjustified. Therefore, in calculating the total amount of energy involved in various items of the budget of an average 1972 male or female *B. gigas*, the starting date is that at which the population reached an average length of 20 mm—*viz.* 30 April. A cumulative energy budget (see Klekowski, 1970) for *Branchinecta gigas* from 30 April to 15 June 1972 is given in Table XVI.

It is apparent from the table that despite the many errors involved in measurement of all these parameters, the estimated energy consumption of an animal during most of its life cycle was adequate to account for all of the energy being used over that period. In other words, the budget is positively balanced. The absolute value of each parameter, of course, is of dubious accuracy, but it is likely that the relative distribution of ingested energy among the different functions is similar to that actually occurring.

Summation of the energy output values (excluding faecal losses) provides widely differing estimates of assimilation efficiency (Ingestion-Faecal losses) between males and females (Table XVI). In other crustaceans, assimilation efficiency varies from 13-32% in *Daphnia* (Richman, 1958) to more than 90% in *Calanus finmarchicus* (Marshall and Orr, 1955) and the mysid *Metamysidopsis elongata* (Clutter and Theilacker, 1971), and it is probable that most carnivorous Crustacea exhibit at least 60% assimilation efficiency (Conover, 1966). Examination of intestinal contents in this study indicated that only the integument and gut contents of the prey remained visible in the hindgut region of *B. gigas*;

all muscle, oil and body fluids had apparently been absorbed. An estimate of assimilation efficiency in excess of 90%, therefore, is probably not unreasonable.

The lower estimate of assimilation efficiency in males may or may not be valid. As noted before, a single *B. mackini* represents a large quantity of energy in relation to the daily requirements of the predator. Hence, measurement of energy consumption by *B. gigas* using this prey alone is necessarily imprecise. On the other hand, measurements of the rate of leg movement in males and females at the same temperature showed that the former rate was 8-15% faster than the latter. If, as suggested above, the rate of ingestion is related to the frequency of contact with potential prey, the rate of feeding and defaecation should be proportionately higher in males than in females, and the assimilation efficiency relatively lower. This effect has been well documented in *Artemia salina* (Reeve, 1963*a*,*b*) and is a feature worthy of examination in *B. gigas*.

The partitioning of assimilated energy, however, does show close similarity between the sexes. Thus, the proportion of assimilated energy expended in growth, excretion, and to a lesser extent, moulting, is approximately the same in males and females. The major difference is in terms of respiratory loss, where it would seem that egg production takes place at the expense of metabolic rate. Put another way, the male invests an equivalent fraction of available energy in functions directly affecting respiratory rate to the proportion invested by females in egg production. As mentioned above, males are notably more active than females.

TABLE XVI. Cumulative Individual Energy Budget for *Branchinecta gigas*, Eyeeinghorse Lake, 30 April - 15 June, 1972.

Parameter	Symbol	MALES cals.	%C	%A	FEMALES cals.	%C	%A
Ingestion	C	1088.0			1452.1		
Growth	P_g	165.3	15.2	21.3	297.3	20.5	21.2
Reproduction	P_r				112.5	7.7	8.0
Moulting[1]	E_x	81.3	7.5	10.5	159.5	11.0	11.4
Respiration	R	427.4	39.3	55.2	643.0	44.3	45.8
Non-faecal[2] Excretion	U	100.8	9.3	13.0	190.4	13.1	13.6
Assimilation[3]	A	774.8	71.3		1402.7	96.6	

[1]Based on data of Khmeleva (1967), Wissing and Hasler (1968).

[2]Based on data of Bernice (1972*a*).

[3]Derived as sum of P, E_x, R and U.

No equivalent data are available for ingestion or assimilation during 1971. The average maximum length attained by males and females was 60.8 and 72.4 mm, representing 355 and 519 calories, respectively. If one assumes that the same proportion (21.3%) of assimilation was invested in growth in both years, a tentative estimate may be made of the partitioning of energy between maintenance costs (respiratory loss) and reproduction in 1971. It is presumed that each female, on average, produced two broods with an average of 468 eggs in each (see Fig. 10). These calculations are summarised in Table XVII, and it would appear that the percentage of assimilated energy lost in respiration by a male is not greatly different from the sum of respiratory loss and reproductive output by a female.

While the construction of a budget for the whole life cycle provides some insight into the energy relations of the organism, it gives no information about the way in which available energy is distributed among necessary functions at different times. For example, the majority of growth takes place during the first half of the life cycle, whereas most of the respiratory losses and all reproductive activity take place during the latter half. Therefore, in order to examine the expenditure of energy as a function of time, each of the three major parameters measured in 1972 (growth, ingestion and respiration) have been recalculated on a *per diem* basis. The results, covering the period from 30 April to 15 June are shown in Figure 25. It must be emphasised that all of the original data were expressed in relation to the length and fitted to straight lines either in arithmetic or logarithmic forms. Thus, any change in the pattern of these

TABLE XVII. Partitioning of Assimilated Energy by *Branchinecta gigas*, Fleeinghorse Lake, 10 May - 14 June 1971.

	MALES		FEMALES	
Parameter	cals.	%A	cals.	%A
Assimilation[1]	1667		2438	
Growth	355	(21.3)	519	(21.3)
Reproduction			229	9.4
Respiration	355	21.3	354	14.5

[1]By calculation, assuming Growth equalled 21.3% of A.

Figure 25. Changing patterns of energy expenditure during the life cycle of *Branchinecta gigas*, 1972.

Black - Energy expended in growth per day.

Hatched - Energy lost in respiration per day.

——— - Estimated energy ingested per day.

MALES
FEMALES
CALORIES PER DAY
45
40
35
30
25
20
15
10
5
0
MAY
JUNE
1972
MAY
JUNE
1972

relationships at sizes greater than 20 mm would have been obscured. No such changes were evident in the data, but often variability of the results was high. Obviously, the regularity of distribution through the two compartments shown is primarily a function of this straight-line reduction to length and the use of fitted logistic growth curves.

Growth (black) and respiration (hatched) compartments in Figure 25 have been drawn cumulatively, so that the amount of energy used in respiration on any given date is represented by the distance between the upper edges of the black and hatched areas, respectively. Correspondingly, the total amount of energy used for maintenance during the life cycle period covered is given by the hatched area, and total investment in growth by the black area. The figure demonstrates clearly how the partitioning of available energy varies during the life cycle. In accordance with changing growth rate, deposition of body tissue reaches a peak on May 12, representing energy expenditures of 11 and 18 calories per day for males and females, respectively. In contrast, maintenance costs increase throughout the life cycle, and in later weeks represent a larger fraction of the total expenditure.

The amount of energy actually consumed, as determined from feeding experiments and proportion derived naturally from *B. mackini* (Fig. 24) is shown by the single black line in each graph of Figure 25. It is apparent that during the second week in May this estimate of energy intake is not high enough to account for all of the energy lost in respiration and accumulated in growth, regardless of losses in faeces, urine and ecdysis. The inadequacy may be partly attributed to the procedure of reducing data to a length basis, but primarily to a lack

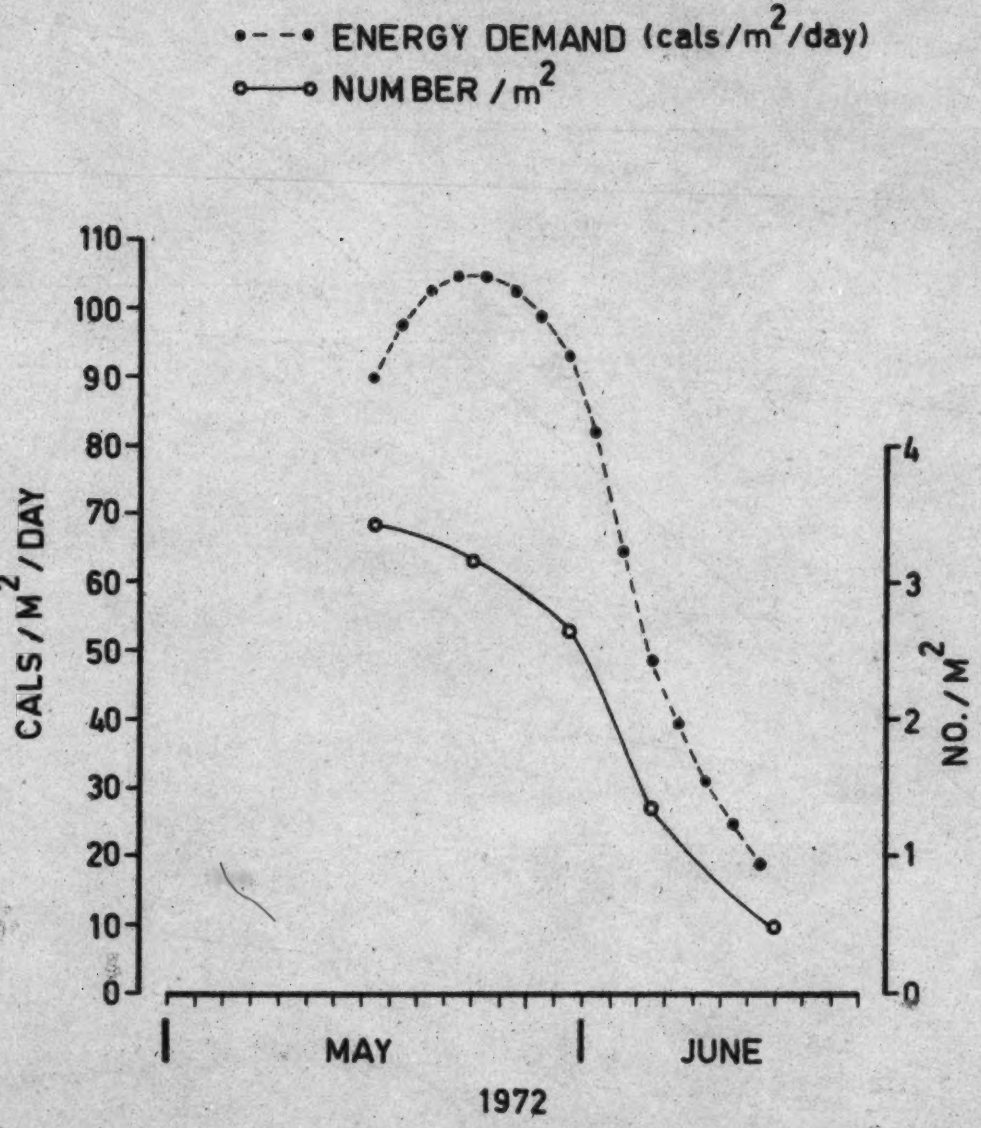
of precision in assessing energy consumption of animals in smaller size groups.

Many of the estimates upon which these two versions of the individual budget were based require closer experimental examination before their accuracy can be determined. In particular, more sophisticated methods are required for the determination of ingestion rate and oxygen consumption, as well as an independent measurement of faecal losses. Nevertheless, the relative distribution of energy among different functions is conformable with data acquired in other studies of crustaceans (cf. Clutter and Theilacker, 1971), and is in accord with expectations. For example, it was anticipated that the proportion of energy invested in growth would be considerable, and that most of this investment would be made during the first half of the life cycle. By comparison, less than 5% of assimilated energy is involved in growth during the entire life of 130 days in *Artemia*, whereas 27% is used in the production of eggs (Khmeleva, 1967). The different patterns thus shown by *Artemia* and *B. gigas* are clearly correlated with different life styles.

Population Energetics

Reservations have been expressed above regarding the reliability of population density estimates of *B. gigas* (Table VII) and of values for total energy consumed (Fig. 25). With these limitations in mind, the two sets of data have been combined to provide an account of the demand placed upon its food supply by the population during the period for which density estimates were available. In Figure 26 the values of population density listed in Table VII have been plotted according

Figure 26. Population density and energy demand of *Branchinecta gigas*, Fleeinghorse Lake, 1972.


ENERGY DEMAND (cals/m²/day)
NUMBER / m²
CALS / M² / DAY
NO. / M²
110
100
90
80
70
60
50
40
30
20
10
0
4
3
2
1
0
MAY
JUNE
1972

to the date and joined by a smooth curve fitted by eye. Using these values and interpolating for dates between samples, the estimated number of *B. gigas* on every second day was multiplied by an average value for energy consumption on each occasion obtained from Figure 25. The resultant curve describes the changing energy demand of the population. It is to be noted that the highest demand of 105 cals/m^2 per day occurs about 23 May, and coincides with the peak biomass value for *Branchinecta mackini* of 2700 calories per square metre.

ARGILLOTROPHY AND COMMUNITY STRUCTURE

Fleeinghorse Lake is a shallow, semi-permanent body of water occurring as the focus of a small inland drainage (euendorheic) area in a semi-arid region. Dissolved salt concentrations are moderately high and dominated by sulphates. To a considerable extent these categorisations summarise the major physical and chemical features of the lake and the patterns of seasonal change.

The lake receives most of its volume in a short period in spring from snow accumulated over the winter. During the remaining part of the year water volume decreases through evaporation, but in relatively wet summers (such as 1970), local rainstorms may maintain the water level until freeze-up in autumn. Surrounding soils probably have a perennial water deficit and therefore little percolation into the lake through the soil takes place; indeed, capillary 'creep' of water out of the basin may be of greater importance during most summers, since this would remove dissolved salts and deposit them around the perimeter. With decreasing water volume the concentrations of many dissolved ions rise steadily, achieving a two- to three-fold increase during the ice-free months. Such changes do not appear to be critical to the fauna.

Two physical features alone seem to be of paramount importance in characterising the lake as an environment for aquatic life. With such a small volume and large surface area, the basin has minimal capacity for heat storage. Accordingly, for three or more months during the winter all water and at least the surface sediments remain frozen.

All biological activity is thus restricted to the summer and early winter periods: Fleeinghorse Lake is thus an *aestival* lake (Welch, 1952). The processes occurring during freeze-up have not been examined in this study, but may be readily inferred from ancillary observations. With formation of the first ice cover, wind disturbance would greatly decrease and many of the larger suspended solids settle out. Furthermore, declining temperatures would result in crystallisation of mirabilite so that the salinity of the remaining water might also decrease. It is perhaps significant, in this respect, that the only phytoplankton population discovered was found beneath early winter ice, but since few of the invertebrates remained at this time, the importance of this period of primary production to the overall economy of the community remains obscure. In spring, the frozen sediments are the last part of the lake to undergo thawing. Thawing of frozen sediments occurs fairly rapidly throughout each basin and provides a discrete initiation of the season's biological activity. The feature is of considerable importance in terms of the suitability of the lake system as a subject for system modeling and analysis.

The second important physical feature is that of extreme turbidity. Throughout the summer period, suspended solids must prevent the penetration of light beyond a few centimetres except during extended very calm periods. Accordingly, I have been unable to find any evidence of phytoplankton anywhere in the lake during summer. Fleeinghorse Lake is thus an *argillotrophic* environment.

Argillotrophy

The occurrence of water bodies exhibiting persistent, extreme

turbidity has been documented and discussed by Hutchinson (1937), following his surveys in South Africa and the Lahontan Basin region of western North America (Hutchinson *et al.*, 1932; Hutchinson, 1937). Several similar ponds were examined in Algeria by Gauthier (1928—in Hutchinson *et al.*, 1932) and Beadle (1943). They are, perhaps, one of the characteristic aquatic habitats of arid or semi-arid regions, and provide distinct environmental conditions for species inhabiting them. As indicated by observations in this study, most of the suspended solids that prevent light penetration are present in the water column because of continual mixing by wind, but some of the turbidity is the result of colloidal, and possibly bacterial suspensions. Persistent wind disturbance also precludes development of the extensive stratification described by Eriksen (1966*a*); in general, there seems little similarity between the turbid ponds he studied and the truly argillotrophic pans of South Africa and sloughs and playas of North America.

The presence of large quantities of suspended solids in the water column precludes development of phytoplankton populations, but does not prevent the appearance of an extensive aquatic fauna. On the contrary, very dense populations of zooplankton are typical of this type of environment (Hutchinson *et al.*, 1932). Examination of some members of the Fleeinghorse Lake community by myself and of cladocerans from Big Washoe Lake, Nevada by Hutchinson (1937) indicated that feeding was achieved by filtering the suspended particles (or 'feindetritus') from the water. Thus, use of the neologism argillotrophic is perfectly justified. Unfortunately, studies to date have

not identified the precise form in which nutrients and energy are obtained from filtering 'feindetritus'. Several lines of evidence nonetheless indicate that bacteria of one type or another occupy a pivotal position in the flow of energy through the system. Following earlier recognition of the trophic importance of bacteria in estuarine conditions (McGinitie, 1932; Zobell and Feltham, 1942), consideration of bacterial processes in fresh waters has rapidly increased in recent years (e.g. Marzolf, 1965; Felton *et al.*, 1967; Rhee, 1972). Aerobic and anaerobic heterotrophic bacteria are of paramount importance in the mineralisation of organic matter produced by higher plants and animals, and in recycling both the released nutrients and some of the associated energy. Indeed, much primary production by phytoplankton (Saunders, 1972) and by macrophytes (Allen, 1969, 1971; Hobbie, 1971; Wetzel and Manny, 1972) is released into water as dissolved organic compounds and becomes available to secondary consumers primarily through the agency of heterotrophic bacteria. Without their intervention, a high proportion of the energy contained in these substances would be lost to the system (Sorokin, 1965).

The scale upon which such regenerative processes takes place is perhaps much greater than generally recognised. In an oligotrophic lake, for example, Tilzer (1972) determined that heterotrophic productivity was up to 50 times that of phytoplankton during the winter months, and represented as much as one third of photosynthesis over the whole year. In a eutrophic system, however, bacterial production is equal to or greater than photosynthesis (Fischer, 1970).

With respect to the Fleeinghorse Lake system, the apparent absence

of organic matter in bottom sediments (except near *Scirpus* beds) suggests that heterotrophic bacteria succeed in transforming all organic matter derived from production of the zooplankton into bacterial biomass. The rapid disappearance of exoskeletons and faecal material from non-sterile laboratory cultures reinforces this interpretation. Presumably much of this recovered energy is returned to the remaining invertebrates that feed on 'feindetritus', and hence to secondary consumers. As a result, the large quantities of suspended particulate matter play a dual rôle in the dynamic organisation of the system. In the first place, a very large universe is provided as substrate for bacteria, even if only a small percentage of the surface area is actually covered (cf. Hargrave, 1972). Because of the absorptive properties of clays and clay-like particles (Lee, 1970), such a site is probably ideal for heterotrophic microfloral growth. Secondly, the particles themselves provide an effective mechanism for collection of the bacteria present. Undoubtedly, part of the reason for the large invertebrate biomass achieved in Fleeinghorse Lake is the rapid and efficient recycling of energy and nutrients from organic material in the bodies of dead animals. Nevertheless, while the regenerative process may be extremely efficient, it is concerned with utilisation of material that has already been fixed in animal or plant biomass; the origin of the energy necessary to form that biomass must still be explained.

The second major rôle played by bacteria in lake systems is associated with oxidation of the products of anaerobic decay, and the incorporation of the energy obtained into synthesised organic

compounds. This is perhaps most familiar with respect to the oxidation of hydrogen sulphide to sulphate by a variety of colourless sulphur bacteria and thiobacteria. The energy released in the two-step oxidation is considerable: 202 calories for each molecule of hydrogen sulphide converted to sulphate (Ruttner, 1953). Under anaerobic conditions, the reverse reactions are effected by bacteria using energy derived from organic material (e.g. *Desulfovibrio*) or directly from sunlight (e.g. *Chromatium* and *Chlorobium*). Presumably the black, sapropel-like deposits near *Scirpus* beds in Fleeinghorse Lake represent the use of organic matter released from the bulrushes for reduction of sulphates. The quantities of sulphur compounds thus produced by bacterial populations may be very high, and deposits of elemental sulphur formed by bacterial action have supported moderately large industries in the past (Butlin and Postgate, 1954; Nriagu, 1968). Furthermore, the co-occurrence of sulphur-oxidising and sulphur-reducing bacteria in 'plates' at the boundary between aerobic and anaerobic water is almost a *sine qua non* of meromictic saline lakes (Trüper and Genovese, 1968; Bradbury, 1971; Benoit *et al.*, 1971).

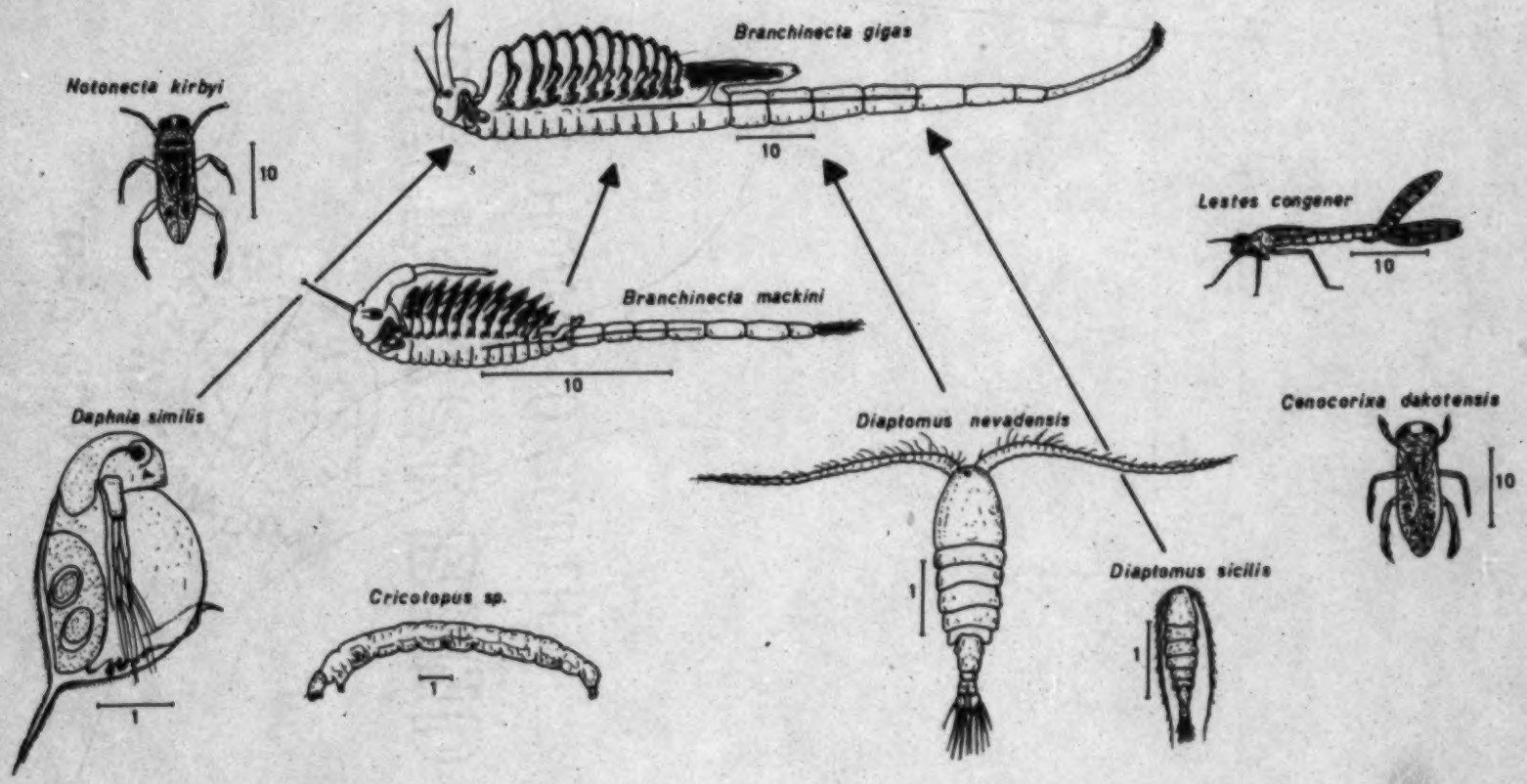
It is perfectly feasible, though as yet unproven, that both heterotrophic and chemotrophic functions of bacterial populations are of fundamental importance to the dynamic organisation of the community in Fleeinghorse Lake. Certainly the rates of bacterial production detected in other aquatic systems are sufficient to explain the high rates of growth and high biomass of invertebrates in this lake. The primary origin of this energy is still unknown, but two possibilities present themselves, both of which would require special study. The importance

of the well-known purple and red sulphur bacteria was originally recognised after the highly coloured plaques were seen in the clear waters of saline meromictic lakes. No such organism could have been detected in Fleeinghorse Lake without a specific search, and so some phototrophic sulphate reduction might be taking place, particularly beneath the first ice cover in autumn. Reduced forms of sulphur might then remain until the following spring. It may be remembered, in this connection, that a large population of the photoautotroph *Phacus* occurred at this time. An alternative source may be allochthonous organic material from surrounding fields either introduced during spring thaw or by wind action (afflation) during the summer. Neither of these possibilities seems adequate to explain the extensive community present in the lake, but each is worthy of much closer examination.

Community Structure

Irrespective of the primary energy source, it is apparent from this study that the main pathway to the invertebrate members of the community is through the 'feindetritus' that is so characteristic of the lake. In Figure 27 the major species forming the community are presented to show the energy pathways that have been considered. Of the nine species shown, it is presumed that four (*B. gigas*, *N. kirbyi* *L. congener* and *D. nevadensis*) obtain their energy wholly or partly by predation upon the other members of the community. With exception of the corixid and possibly *Cricotopus*, the other species filter suspended solids and their associated microflora from the water. It is interesting to note the similarity between this community and the

Figure 27. Major components of the community in Fleeinghorse Lake. Scales indicated in millimetres.


Branchinecta gigas
Notonecta kirbyi
10
10
Lestes congener
10
Branchinecta mackini
10
Daphnia similis
Diaptomus nevadensis
Cenocorixa dakotensis
10
1
Cricotopus sp.
1
1
Diaptomus sicilis
1

communities of other argillotrophic lakes: "A peculiar association of *Daphnia*, a large and a small Diaptomid, is characteristic of extreme cases [of argillotrophy], and is found in various parts of the world" (Hutchinson, 1937, p. 115). Hutchinson further noted the possibility of phyllopod populations in the early spring in Big Washoe Lake, although none were present at the time of his visit. Hutchinson *et al.* (1932) also recorded that lakes of this type in South Africa were deficient in phytoplankton except for the sporadic occurrence of euglenoids, and exhibited a sparse chironomid fauna. Undoubtedly the latter is related to the low organic content of bottom sediments, and therefore to the efficient regenerative processes at work.

Necessarily, the present study has only begun the process of dissecting the community to trace patterns of organisation, and the only energy pathways that have so far been measured relate to partitioning within individual *Branchinecta gigas*. Nonetheless, an impression of efficient energy transfer has emerged. Estimates of energy intake and expenditure indicate that a high percentage of ingested food was assimilated—perhaps more than 90% in females. Of this amount, approximately one fifth was deposited as body tissue, which is almost half of that lost in maintenance. Perhaps 10 per cent was used in production of eggs, which represents an investment by the species to guarantee persistence into the next season. The extremely high growth rates observed in both *Branchinecta gigas* and *B. mackini* would clearly be most appropriate if the primary energy source was made available in the early spring and not greatly supplemented thereafter. Furthermore, the organic matter thus synthesised

was apparently recirculated rapidly upon death of the animal. Finally, the one interaction studied in any detail, that occurring between the two species of fairy shrimp, revealed a very close coordination between them. Thus, the major energy demand of the *B. gigas* population coincided with the greatest biomass of an important prey species—*B. mackini*.

These fragments of pattern attest to the close adjustment of the community to the conditions of its environment. If, as is generally assumed, there is a trend in community evolution toward maximum utilisation of available energy, one would expect the development of a seasonal succession of species. To some extent, this occurs in Fleeinghorse Lake, since reproduction in *Daphnia similis* and the two diaptomids begins immediately after the decline of fairy shrimp populations in mid-summer. Late-season production, however, does not compare in magnitude with that of April and May. This is precisely the pattern that might be expected in a system receiving its main energy supply at the beginning of the season and having little capacity to store such energy for subsequent use—except in the form of animal biomass.

* * * * *

Ecological research into the organisation of natural communities has followed two distinct paths in recent years. The analytical approach is aimed at dissection of a natural community into its functioning sub-units, the identification of important interactions between them and deduction of the way in which integration of the sub-units provides stability of the whole. Such an approach is evident

in the work of Lindeman (1942), Odum (1957), Margalef (1968) and many others. An alternative viewpoint, typified by the studies of Beyers (1963), Hairston *et al.* (1968), Cooke (1971) and Taub (1971) is essentially synthetic in that the attempt is made to reconstruct a relatively stable system from elementary units. Clearly the two approaches are complementary, but at present operate upon totally different levels: the sub-units used in an analytical study are usually multi-species groups or trophic levels, whereas laboratory microcosms are constructed from a few individual species only. It seems obvious, therefore, that the analysis of relatively simple communities, such as that inhabiting an argillotrophic lake, provides an appropriate third alternative.

The results of the present study clearly require reaffirmation and augmentation. Nonetheless, a number of advantages are already evident for using the argillotrophic lake community for system analysis. The discrete origin of seasonal activity resulting from total freezing during the winter provides a convenient and natural starting point. Following hatching, all three species so far studied exhibit patterns of growth that are readily fitted to simple mathematical formulae, allowing assessment of the status of individuals in any species to be predicted at any point in time. With more data on biomass changes, it should be possible to describe and predict the changing status of populations as well. Finally, the number of sub-units involved in the community is sufficiently small to be subjected to meaningful computer simulation.

Even at this stage, a number of important problems in explaining

the organisation of the community may be identified. It is apparent that bacterial populations are of fundamental importance to the patterns of energy flow, but the primary origin of the energy remains obscure. If much of this proves to have a chemosynthetic origin, the importance of the system for controlled food production becomes obvious. As mentioned above, the present, admittedly incomplete, results show a pattern of secondary production that is predictable in dynamic theory if the community was provided with a single energy input at the beginning of the season. Natural selection of members of the community might then be for species that exhibit rapid growth rates in order that maximum use is made of a transient food supply. Solutions to some of these problems must lead to a more complete understanding of this simple community, and probably would provide valuable insight to essential processes in more complex ecosystems.

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APPENDIX I. Provisional list of species collected from Fleeinghorse Lake, 1969 - 1972.

TAXON	SPECIES	NOTES
Crustacea		
Anostraca	*Branchinecta gigas*	r; ++.
	Branchinecta mackini	r; +++.
	Eubranchipus bundyi	n; rarely washed in from nearby pool.
Notostraca	*Lepidurus lemmoni*	r?; mature specimens collected only in June, 1969.
Conchostraca	*Lynceus brachyurus*	n; juveniles washed in from nearby pool each spring.
Cladocera	*Daphnia similis*	r; +++.
	Daphnia parvula	n; collected only July and Oct. 1972.
	Daphnia rosea	n?; occasional 1971 and 1972.
	Daphnia pulex	n?; common in June/July 1972.
	Simocephalus vetulus	n; collected once only, June 1971.
	Polyphemus pediculus	n; collected once only, Aug. 1969.
Copepoda	*Cyclops vernalis*	n?; probably washed in from nearby pool each spring.
	Diaptomus nevadensis	r; ++++.
	Diaptomus sicilis	r; +++.
Insecta		
Collembola		unidentified; very abundant on surface 1971 and 1972.
Odonata	*Lestes congener*	r; +.
	Lestes dryas	r?; collected only in July 1972.
Hemiptera	*Notonecta kirbyi*	r; ++.
	Cenocorixa dakotensis	r; ++.
	Cenocorixa utahensis	n; collected only August 1969.
	Corisella tarsalis	n; collected only August 1969.
	Callicorixa audeni	n; collected only August 1969.
	Trichocorixa verticalis	n; collected only August 1969.

APPENDIX I (cont'd)

TAXON	SPECIES	NOTES
Insecta (cont'd)		
Coleoptera	*Dytiscus* sp.	r; +.
	Hygrotus masculinus	r; +.
	Hygrotus semivittatus	r; +.
	Haliplus sp.	n?; rarely encountered
Diptera	*Chironomus atrella*	r; +.
	Cryptochironomus sp.	r; +.
	Cricotopus sp.	r; +.
	Procladius sp.	r; +.
	Ablabesmyia sp.*	r; +.
	Ceratopogonidae	r; ++.
Mollusca	*Physa* sp.	n?; collected once only, June 1971.

*(possibly *Ablabesmyia peleensis* or *A. illinoiensis*).

KEY	:	r	resident	n	non-resident
		+	uncommon	++	common
		+++	abundant	++++	very abundant

APPENDIX II. Comparison of logistic, Gompertz and von Bertalanffy growth curves with observed growth of *Branchinecta gigas*, *B. mackini* and *Diaptomus nevadensis* in Fleeinghorse Lake.

A variety of theoretical curves have been proposed to describe the patterns of increase in weight exhibited by organisms. Where the accumulation of biomass during the life span of an individual may be represented by a sigmoid curve, three separate formulae describing slightly different forms of the generalised curve have each been used considerably in interspecific and intraspecific comparisons of growth, and as a basis for analysis of the dynamic properties of populations. These standard curves are defined by the logistic, Gompertz and von Bertalanffy formulae, and differ primarily in the position of the point of inflection in relation to the asymptote, and in the rate at which the asymptote is approached during the latter part of the growth period. A convenient and simple graphical method has recently been provided by Ricklefs (1967) that allows comparison of empirically observed patterns of growth with each of these three theoretical curves.

For each curve, Ricklefs calculated the conversion factors that were required to adjust the value for weight at each instant (expressed as a percentage of the asymptote) to fit a straight line tangential to the growth curve at the point of inflection. Thus, the essence of his method is that the empirical values for weight obtained at intervals during the life cycle are first transformed into percentages of the asymptote, and the conversion factors corresponding to these percentages for each theoretical curve are then plotted against time. The most appropriate growth formula is therefore determined as that for which

the conversion factors provide the closest fit to a straight line. Conversion factors of less appropriate formulae exhibit curvature throughout their range.

There was no *a priori* reason to assume that any one of the three curves would provide the most satisfactory fit to the patterns of growth observed in field populations. This is true even though the curve devised by von Bertalanffy was at least partly based upon laboratory studies of *Artemia salina* (von Bertalanffy and Krywienczyk, 1953) and other fresh water crustaceans (von Bertalanffy, 1957). Therefore, the growth curves for males and females of *Branchinecta gigas*, *B. mackini* and *Diaptomus nevadensis* were compared with each of the logistic, Gompertz and von Bertalanffy formulae for each year that data was available. The results are shown in Figures A1, A2 and A3.

In each case the basic data were mean lengths obtained from Fleeinghorse Lake samples collected at varying intervals during the life cycle. As a result, each value is subject to such influences as sample size variation, differential mortality according to sex or age, and variation in water temperature. It was to be expected, therefore, that for each theoretical curve the plotted conversion factors would not adhere strictly to a straight line, but would at best vary around one. It is clear from these graphs, nonetheless, that the logistic formulae always provided the closest fit to the observed pattern of growth; both the Gompertz and von Bertalanffy conversion factors consistently show an upward curvature when the whole life cycle is considered.

Figure A1. Comparison of the observed growth of *Branchinecta gigas* in Fleeinghorse Lake with the logistic, Gompertz and von Bertalanffy curves, 1970 - 1972.

Logistic (L) o--------o

Gompertz (G) +————→

von Bertalanffy (B) ●·····●

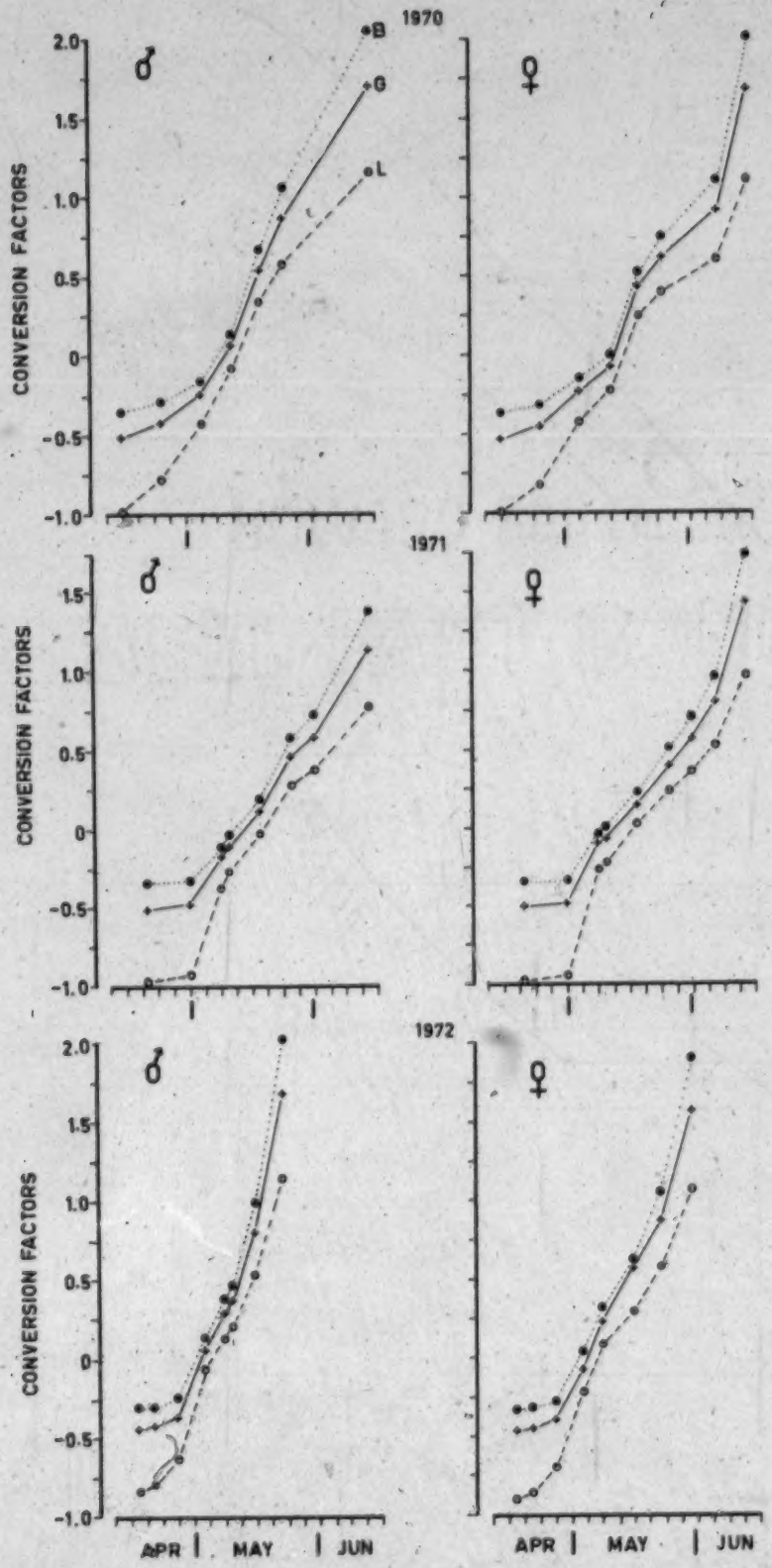
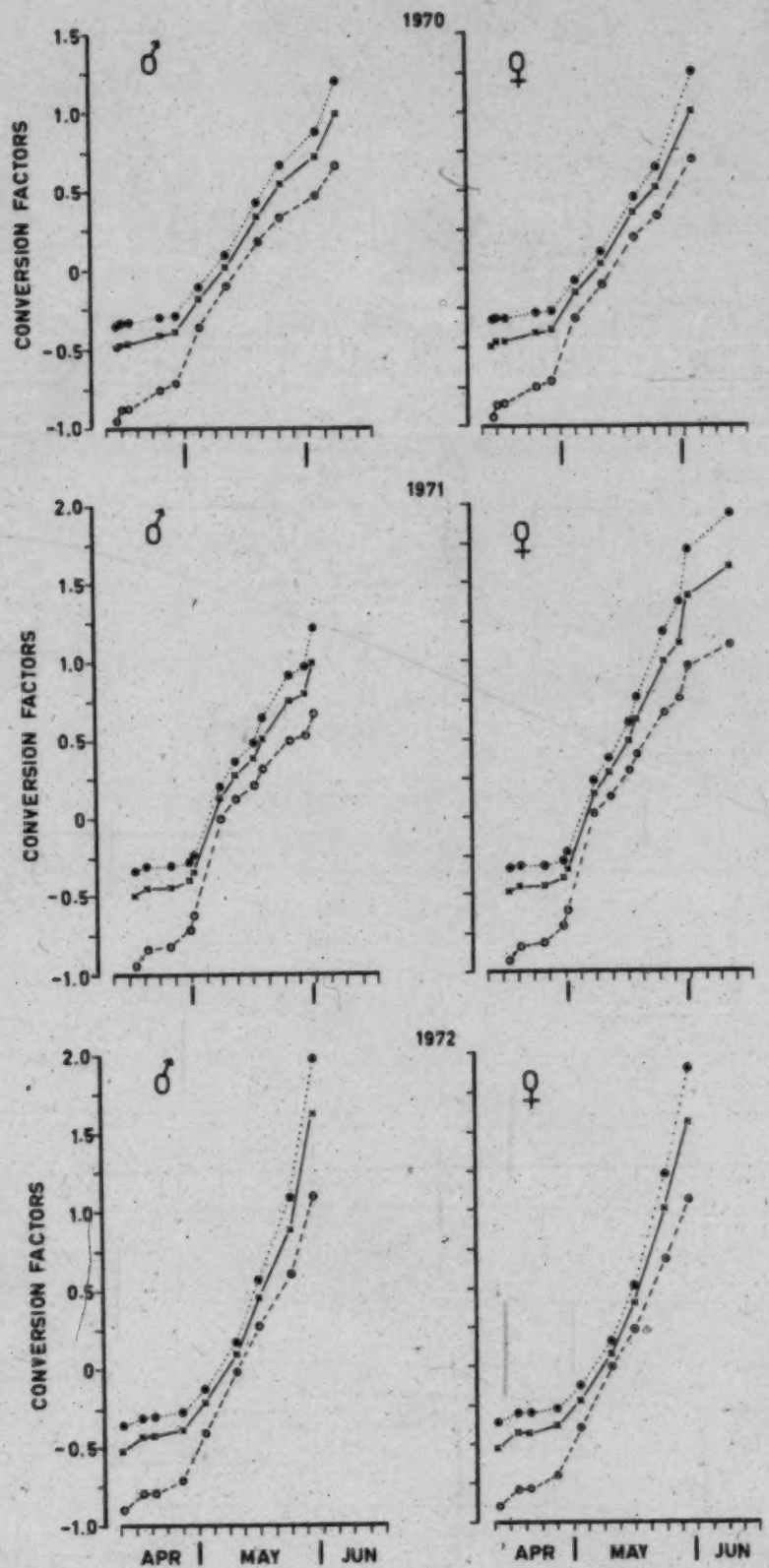

1970
1971
1972
♂
♀
B
G
L
CONVERSION FACTORS
2.0
1.5
1.0
0.5
0
-0.5
-1.0
APR
MAY
JUN

Figure A2. Comparison of the observed growth of *Branchinecta mackini* in Fleeinghorse Lake with the logistic, Gompertz and von Bertalanffy curves, 1970 - 1972.

Logistic (L) o--------o

Gompertz (G) +————————+

von Bertalanffy (B) ●·····●


1970
1971
1972
♂
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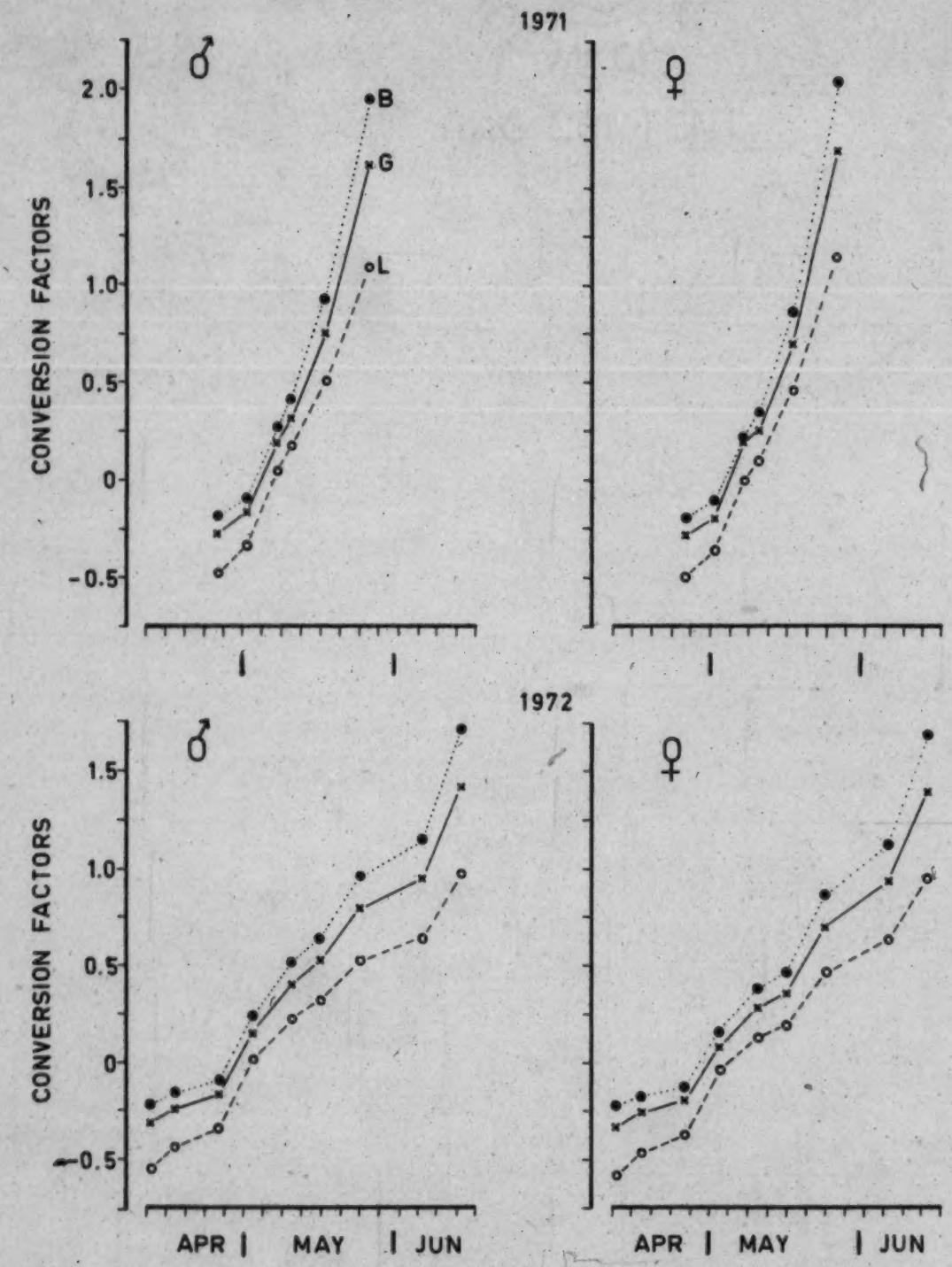
CONVERSION FACTORS
1.5
1.0
0.5
0
-0.5
-1.0
2.0
APR
MAY
JUN

Figure A3. Comparison of the observed growth of *Diaptomus nevadensis* in Fleeinghorse Lake with the logistic, Gompertz and von Bertalanffy curves, 1971 and 1972.

Logistic (L) o--------o

Gompertz (G) +————————+

von Bertalanffy (B) •••••••••


1971
♂
♀
B
G
L
2.0
1.5
1.0
0.5
0
-0.5
CONVERSION FACTORS
1972
APR
MAY
JUN

The greatest influence on the actual form of the sigmoid curve is the pattern of early growth; under field conditions, the relatively slow change in average length at this time is the result of continuous hatching over a period of several days, and the low water temperatures prevailing. As shown in Figure A1, the importance of these influences may vary considerably from year to year as the pattern of thawing in the lake varies. Thus, for both sexes of all three species examined, the logistic curve provides the closest approximation in each year that data were examined.

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APPENDIX III. Quantitative samples obtained from Fleeinghorse Lake, 1971.

Date	Basin	Sample	Depth	Males	Females	Total	No./m^2
May 19	E	E	111.0	69	60	129	304.9
	C	D	91.7	33	37	70	165.5
		F	107.5	6	3	9	21.3
		G	100.6	14	16	30	70.9
	W	A	88.9	12	22	34	80.4
		B	88.9	14	21	35	82.7
		C	86.8	7	16	23	54.4
June 1	E	A	97.3	24	23	47	111.1
		C	102.2	13	16	29	68.6
	C	D	116.0	17	29	46	108.7
		E	105.3	17	18	35	82.7
		I	87.5	6	15	21	49.6
	W	F	81.5	14	24	38	89.8
		G	83.3	11	16	27	63.8

APPENDIX IV. Quantitative samples obtained from Fleeinghorse Lake, 1972

Date	Basin	Sample	Depth	NUMBER IN SAMPLE Haul#1	Haul#2	Total	No./m^2
May 10	E	A	98.0	21	16	37	87.5
		C	103.0	34	27	61	144.2
		F	108.5	34	38	72	170.2
	C	G	108.5	27	42	69	163.1
		H	106.0	39	25	64	151.3
		N	77.0	23	29	52	122.9
	W	J	69.0	46	41	87	205.7
		K	67.0	38	51	89	210.4
		M	64.5	19	34	53	125.3
May 16	E	A	80.0	26	31	57	134.7
		B	82.0	29	27	56	132.4
		D	82.0	11	14	25	59.1
	C	E	83.0	22	24	46	108.7
		F	81.0	29	24	53	125.3
		L	82.0	22	21	43	101.6
	W	G	66.0	28	27	55	130.0
		J	67.0	16	30	46	108.7
		K	78.0	34	26	60	141.8
May 23/24	E	23A	92.0	15	22	37	87.5
		B	75.5	14	28	42	99.3
		C	99.5	18	21	39	92.2
	C	24A	91.0	31	36	67	158.4
		B	81.0	26	20	46	108.7
		C	83.0	23	26	49	115.8
	W	E	61.0	24	25	49	115.8
		F	65.5	24	29	53	125.3
		G	67.0	9	23	32	75.6

APPENDIX IV (cont'd)

Date	Basin	Sample	Depth	NUMBER IN SAMPLE Haul#1	Haul#2	Total	No./m^2
May 30/31	E	30A	85.5	11	13	24	56.7
		C	82.0	26	13	39	92.2
		D	96.0	13	11	24	56.7
	C	F	72.0	8	4	12	28.4
		G	86.0	12	28	40	94.6
		H	77.0	17	39	56	132.4
	W	31A	59.5	6	10	16	37.8
		C	65.5	16	16	32	75.6
		D	64.5	18	6	24	56.7
June 5/6	E	5B	45.0	7	16	23	54.4
		C	72.0	5	2	7	16.5
		D	89.5	0	1	1	2.4
		E	84.5	7	8	15	35.5
		6M	88.0	0	2	2	4.7
	C	A	88.5	1	1	2	4.7
		B	69.5	5	6	11	26.0
		C	74.5	2	0	2	4.7
		D	65.5	5	3	8	18.9
		L	60.5	8	4	12	28.4
	W	F	60.0	7	4	11	26.0
		H	58.5	3	5	8	18.9
		J	57.0	23	16	39	92.2
		K	66.5	15	15	30	70.9
June 14	E	A	86.0	3	1	4	9.5
		C	79.0	16	6	22	52.0
		D	81.0	2	1	3	7.1
		E	90.0	0	7	7	16.5

APPENDIX IV (cont'd)

Date	Basin	Sample	Depth	NUMBER IN SAMPLE Haul#1	Haul#2	Total	No./m^2
June 14	C	F	82.0	11	3	14	33.1
		G	83.0	5	2	7	16.5
		J	74.0	3	4	7	16.5
		K	63.0	4	3	7	16.5
	W	L	56.0	5	10	15	35.5
		N	56.0	21	16	37	87.5
		P	59.0	3	8	11	26.0
		Q	60.0	6	9	15	35.5
June 19	E	A	71.5	1	1	2	4.7
		B	66.0	1	2	3	7.1
		C	80.5	2	0	2	4.7
		E	74.0	3	0	3	7.1
	C	F	90.0	14	3	17	40.2
		H	84.0	6	1	7	16.5
		J	81.0	4	2	6	14.2
		K	61.5	3	3	6	14.2
	W	L	58.5	1	1	2	4.7
		N	56.0	8	1	9	21.3
		P	51.0	2	13	15	35.5
		Q	54.5	1	2	3	7.1

APPENDIX V. Gut contents of *Branchinecta gigas*.

(m = male; f = female; e = *mackini* eggs present;
? = sex undetermined; * = collected Czar Lake, 1970)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
(a) Juveniles:					
2.60					"feindetritus"
2.90					"
3.00		1			"
4.10	1?	2			
4.50					old exuvium
(b) Males:					
5.30					"feindetritus"
5.80					"
6.60*	2?				
14.65	2?	2			
15.00	1?				
24.05	1?	11			
26.10	1?	5			
28.85	2?	12			
31.30	1?	2			
33.50*		22			
33.80	1?	9			
36.40	1?	9	1		
37.30				2	
37.80		3		27	

APPENDIX V (cont'd)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
Males (cont'd)					
38.05		1		1	old exuvium
38.75		3		13	1 *Lestes* sp. nymph
38.75*		22			
39.65	2m				
39.65		13	1	7	
39.80		3		2	
41.90*		29			
42.00		11		7	
42.80		22		2	
43.30	2f	16			
43.30	1m	14		2	
43.60		1			
43.70		7		3	
44.85		9	1	7	
45.35	1f	23			
45.40		7		2	
45.45		13		45	
45.70*		19		2	
45.85	1m	1			
45.85		13		47	
46.05		3			
46.10		5		11	

APPENDIX V (cont'd)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
Males (cont'd)					
46.25*	1?	1			
46.40				19	
46.55	1f	6			
47.15*		17		1	
47.60	2	23			
47.60*		16		1	1 chironomid larva
47.80		44			
48.15*	1fe	2		2	
48.30		21			
48.35*	1?	31		6	
48.45*	1?	10			
48.50		40		11	
48.80	1m	1			
48.85*	2fe	9		1	
48.95		8		17	
49.00*	2?	4			
49.10		4		2	
49.20		18		6	
49.55*	1m	7			
49.60*		22	1		
49.95*		16		2	
50.10*	1fe	12		1	

APPENDIX V (cont'd)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
Males (cont'd)					
50.15*	1fe	20			
50.90		1		10	
50.90		25		19	
50.90*	1m	16		1	
51.70*	1m	16			
52.60		4		14	
53.85		10		18	
55.30*		23			
58.20	1m	14		20	
(c) Females:					
5.60					"feindetritus"
5.80					"
6.30					"
13.10	1?				
15.40	3?				
17.30		5			4
19.00	2?	4			
19.00	3?	4			
20.15	4?	1			
22.65		10			
23.45	1m	4			

APPENDIX V (cont'd)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
Females (cont'd)					
25.60		8			
29.15	2mf	9			
31.50					(large melanin deposit on legs)
34.90		15			
36.45	2f	8		1	
37.85		14	14	2	
41.15	1m	9			
43.20		3		1	
44.60		10		1	
44.80		16		32	
45.30		3	2	2	
47.60		33	2	1	
47.85		23		16	
48.35		10			
49.15*	2f	21			
50.80	2mf	5		1	
51.10		107			
51.95		46		6	
52.00		2		23	
52.10*		15			
52.10	1m	3			
52.65		15		1	

APPENDIX V (cont'd)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
Females (cont'd)					
53.70		12			
54.20		9			
55.15	1f	9			
56.10	1?	13		1	1 chironomid pupa
56.30		24		46	
56.50*	1?	6			
56.60	2?	23		1	
57.05	1?	9			
57.05*	2?	11			
57.50	1m	11		11	
57.60		58	1	6	
57.80	2mf	27			
58.55	2f?	6			
58.85*	1?	26		1	
59.35*	2m?	34		1	
60.40*	2??	47			
60.65*		51			
60.90*	2??	24			
61.20*	1m	7			
61.75*	1m	15		3	
64.10	2mf	6		2	
64.55	1f	4		4	

APPENDIX V (cont'd)

LENGTH (mm)	*Branchinecta mackini*	*Diaptomus nevadensis*	*Diaptomus sicilis*	*Daphnia*	Others
Females (cont'd)					
64.65		16		49	
64.90*	2mf	15		4	
64.90*	3mff	30			1 ostracod shell
65.05*	1m	21			
65.15*		26			
66.55	2mfé	1		2	
66.80	2ffe	4		10	
71.75	2ff				
73.60	1fe	1			
76.00	2mf	7		7	

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APPENDIX VI. Results of feeding experiments with *Branchinecta gigas* in Fleeinghorse Lake, using *B. mackini* as prey.

(a) MALES:

Date	Length of *B. gigas* (mm)	No. *B. mackini* consumed/day	Mean Length of *B. mackini* (mm)	Calories* consumed per day
May 5/6	24.05	5	6.6	0.253
9/10	35.40	10	10.2	9.877
	36.50	11	10.2	11.536
15/16	43.85	4	15.8	16.160
	45.30	3	15.8	12.671
	46.90	6	15.8	25.728
	44.25	1	21.1	12.077
	43.05	3	21.1	35.407
	50.05	4	21.1	46.512
	51.00	4	21.1	46.679
	52.40	1	21.1	11.670
	55.10	4	21.1	47.752
	55.55	2	21.1	23.413
30/31	42.80	1	22.8	14.302
	43.25	5	22.8	70.952
	45.55	4	22.8	57.197
	45.55	5	22.8	70.952
	46.60	5	22.8	68.495
	52.20	2	22.8	27.980
	53.55	2	22.8	28.228
	55.05	1	22.8	13.889
	58.10	2	22.8	28.381
	43.75	2	22.8	27.198
	44.40	4	22.8	54.397
	47.90	1	22.8	13.599
	55.15	3	22.8	40.798
	50.70	5	22.8	67.996
	54.45	2	22.8	27.198

*Time of experiment adjusted to 24 hours.

APPENDIX VI (cont'd)

(b) FEMALES:

Date	Length of *B. gigas* (mm)	No. *B. mackini* consumed/day	Mean Length of *B. mackini* (mm)	Calories* consumed per day
May 5/6	15.40	6	6.6	1.316
	19.00	5	6.6	1.147
	20.15	6	6.6	1.478
	20.35	5	6.6	1.121
	22.65	5	6.6	1.386
9/10	29.80	12	10.2	11.584
	38.75	11	10.2	11.680
15/16	45.80	4	15.8	17.089
	45.80	5	15.8	20.422
	45.95	1	15.8	4.176
	46.00	3	15.8	12.864
	49.65	5	15.8	21.609
	50.55	4	15.8	16.395
	55.15	5	15.8	21.609
	55.30	2	15.8	8.644
	56.55	6	15.8	25.633
23/24	50.15	4	21.1	47.752
	56.80	3	21.1	33.147
	60.25	3	21.1	33.147
	60.75	2	21.1	23.605
	62.35	4	21.1	45.814
30/31	55.55	1	22.8	13.888
	55.85	5	22.8	67.996
	65.20	4	22.8	55.554
June 5/6	52.90	3	22.8	40.798
	55.75	4	22.8	54.398
	57.60	3	22.8	40.798
	58.50	1	22.8	13.599
	60.60	4	22.8	54.397
	66.35	4	22.8	54.397

*Time of experiment adjusted to 24 hours.

APPENDIX VII. Progress of a *Nosema* (Microsporida[1]) epizootic in *Branchinecta gigas* and *Branchinecta mackini*, 1970-1972.

Parasite infections have seldom been recorded in natural populations of fairy shrimp. During May 1970, however, numerous specimens of both *Branchinecta gigas* and *B. mackini* that contained white amorphous masses of microsporidan spores were collected from Fleeinghorse Lake. The percentage of *B. gigas* individuals with such spore masses increased rapidly from 9% on 19 May to 100% by 8 June (Fig. A4). In the *B. mackini* population, 4% showed signs of infection on 11 May and 91% on 3 June; subsequently, however, the percentage infected declined to about 20% when the last *B. mackini* were collected on 24 June. Many fairy shrimp with extensive infections appeared in poor, almost moribund condition, and in view of the decline in infection rate of *B. mackini* during June, it was assumed that mortality was higher in infected than in uninfected animals.

A re-examination of fairy shrimp collections made in 1969 showed no evidence that the parasite had been present in either host population during that year. Presumably, therefore, the infective agent was either introduced into the lake during the summer of 1969 or had been present in another host species occurring in the lake. Occasional *Daphnia* have been found with microsporidan infections in Fleeinghorse Lake, but the identity of the parasite responsible in these isolated instances has not been determined. The epizootic recurred in the fairy shrimp populations during 1971, exhibiting essentially the same

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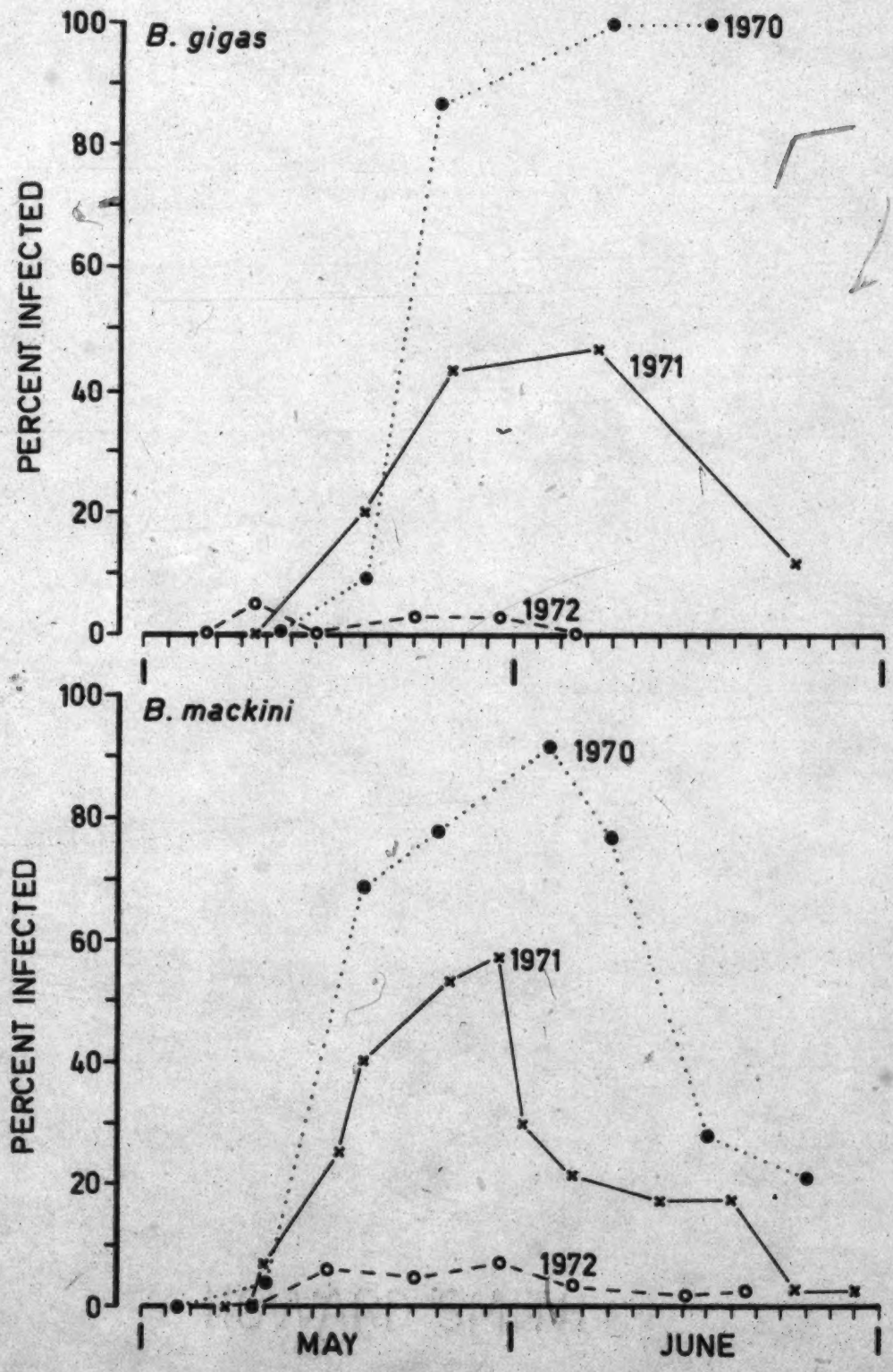
[1]Nomenclature of Honigberg *et al.*, 1964.

Figure A4. Progress of an epizootic of *Nosema* sp. through populations of *Branchinecta gigas* and *B. mackini* in Fleeinghorse Lake, 1970-1972.


B. gigas
1970
1971
1972
PERCENT INFECTED
100
80
60
40
20
0
B. mackini
1970
1971
1972
PERCENT INFECTED
100
80
60
40
20
0
MAY
JUNE

pattern of progress, but at somewhat lower levels than in 1970: infected animals were first collected after 10 May, the percentage with evident spore masses rising rapidly to a maximum of 47% in *B. gigas* (7 June) and 57% in *B. mackini* (30 May), and declining thereafter as infected animals died. In 1972, however, very few infected animals of either *Branchinecta* species were collected, and no distinct pattern in infection rate was evident (Fig. A4).

The parasite has been tentatively assigned to the genus *Nosema*, and further characterisation and description is presently being prepared (W. Brooks, personal communication). The only species of this genus (*N. exigua*) that has so far been described from an anostracan host was recorded from *Artemia sdlina* in Romania; the spores of *N. exigua* were reniform in shape, 2.6μ wide and 3.2μ in length (Codreanu, 1957). In contrast, spores of the *Nosema* infecting *Branchinecta* in Fleeinghorse Lake have a width of 2.4μ, and a length of 4.1μ and are pyriform.

At the present time, the pattern of progress of the epizootic through the fairy shrimp populations cannot be well explained. Almost certainly, infection resulted from ingestion of spores with food material—either in the form of sediment in the case of *B. mackini*, or in the form of *B. mackini* in the case of *B. gigas*. In transmission *per os*, such as this, the spore capsules open and discharge under the influence of host digestive fluids, and the sporoplasm then penetrates the epithelial lining of the gut (Weiser, 1961). Laboratory studies of other species of *Nosema* have indicated that the time from infection to first sporulation varies about one to two weeks: 8-10 days in

N. cuneatum (Henry, 1971) and *N. sphingidis* (Brooks, 1971), and 8-17 days in *N. whitei* (George, 1971; Milner, 1972). Thus, at the lower mean daily temperature of the lake, a generation time of two weeks or more may be postulated for this *Nosema* species. Accordingly, *Branchinecta mackini* probably began ingesting infective spores during the last two weeks of April in each year. The slightly delayed occurrence of the infection in *B. gigas* probably reflects the fact that spores would be obtained from prey animals that had previously ingested them from the water.

There is little evidence available to explain the decreased occurrence of the parasite in 1971 and 1972. An examination of several infected mature female *Branchinecta mackini* indicated that the ovaries and eggs did not contain *Nosema* spores—although schizonts or sporonts may have been present. Transovarial transmission is thus unlikely, although presence of the parasite almost certainly decreased fertility of *B. mackini* and *B. gigas*, and may have reduced the percentage of eggs of each host that subsequently hatched. Differential mortality of eggs, however, may not be the main reason for the lowered levels of infection in the last two years. It is known that spore mortality in another microsporidan, *Thelohania hyphantriae*, increases greatly at temperatures below freezing (Weiser, 1961). It is quite likely, therefore, that the extended period of winter freezing in Fleeinghorse Lake was ultimately responsible for the decreased occurrence of *Nosema* in 1971 and 1972.

Pathology

Many pathological aspects of this host-parasite interaction remain

to be determined from histological examinations that are currently under way. It was evident from the early samples in 1970, however, that large spore masses were most frequently located in certain segments of the thorax, and since many microsporidoses exhibit specific patterns of distribution within the host (Weiser, 1961), it was necessary to characterise the distribution of the new *Nosema*. Accordingly, a number of infected *Branchinecta mackini* collected from Fleeinghorse Lake on 11 and 19 May 1970 were examined, and the location of *Nosema* spore masses in each specimen were recorded. The data are presented in Table AI. It is apparent that spore masses were most often present in thoracic segments 3-5, and with diminishing frequency in segments on either side of the mid-thorax. In the sample examined, no specimens had spore masses anterior to the mandibles (although occasional instances of infection in the head region have been encountered since), and relatively few animals were infected in genital segments. Spore masses in infected *B. gigas* showed a similar distribution and observations of both host species during late May and June indicated that the distribution did not change as the epizootic progressed.

* * * * *

Addendum

A second species of microsporidan was encountered in three specimens of *Branchinecta gigas* from Fleeinghorse Lake, during 1972. Spores of this species are much larger (7.2μ by 3.3μ) than those of the *Nosema*, and infection was characterised by many small, white spore masses distributed throughout the body of the host. Owing to lack of material, this species has not been further characterised.

TABLE AI. Distribution of *Nosema* sp. Spore Masses in Body Segments of Infected *Branchinecta mackini* Collected from Fleeing-horse Lake, 19 May 1970.

Segment	Number of Animals with Spore Masses Present		
	Males	Females	Total
Head	0	0	0
Mandibular/Maxillary	0	2	2
Thorax 1	10	9	19
2	12	12	24
3	15	14	29
4	17	23	40
5	19	21	40
6	9	12	21
7	16	10	26
8	13	7	20
9	11	7	18
10	10	6	16
11	4	5	9
Abdomen 1-2*	5	2	7
3	5	4	9
4	2	2	4
5	1	1	2
6	0	0	0
7	0	0	0
8	0	0	0
9	0	0	0
Number of animals examined	54	55	109

*Segmental division indistinct between genital segments.

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